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Evaluating Survival of Released Ranched American Alligator in Coastal Louisiana

Kristy Durham Capelle
Louisiana State University and Agricultural and Mechanical College

EVALUATING SURVIVAL OF RELEASED RANCHED AMERICAN ALLIGATOR IN COASTAL LOUISIANA

A Thesis

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ABSTRACT

Since 1986, Louisiana's American alligator (*Alligator mississippiensis*) ranching program has required the release of alligators produced from eggs collected from wild nests to maintain wild populations. This project assessed long-term harvest data (1991-2010s) to estimate survival of released alligators. First, wildlife and fishery harvest models and general inter-disciplinary survival models were evaluated to determine best fit to the data. Second, once the best fitting model was selected, release length, precipitation and temperature from release sites, and an index of hunter effort were added to investigate influences on survival estimates. Release length was included because over time the proportion and size of ranch-released alligators has been modified. The generalized linear mixed model, with a fixed intercept, and negative binomial probability distribution was selected as the best fitting model based on the minimization of differences between observed and expected values. This baseline model without covariates estimated instantaneous annual survival to be 0.87 and 0.89, for male and female alligators, respectively. The final best fitting model suggested that the larger an alligator is at release (to a certain point, benefits diminishing after 139 cm), the higher the chance of survival, and the longer it will be afield, for both males ($F_{1,169}$=5.62, p<0.05) and females ($F_{1,180}$=5.89, p<0.05). Mean precipitation was also statistically significant and positively associated with survival of both male ($F_{1,169}$=12.51, p<0.05) and female ($F_{1,180}$=12.33, p<0.05) alligators, suggesting reduced survival in drier years. Additionally, for male alligators, the coefficient of variation for mean temperature was statistically significant ($F_{1,169}$=7.19, p<0.05), suggesting lowered survival during years with more variation in temperature between months. Although not statistically significant, fit of the male model improved with the inclusion of the hunter effort covariate. Inclusion of release length along with environmental and hunter effort covariates improved

precision of survival estimates resulting in values of 0.79 for males, and 0.81 for females, suggesting survival was influenced by the included covariates. Survival estimates with included environmental variables were very similar to reported wild alligator survival estimates, suggesting that ranch-released alligators respond to environmental conditions similar to wild alligators and that ranch-released alligator estimates may provide insights into wild alligator ecology.

CHAPTER 1: EVALUATING SURVIVAL OF RELEASED RANCHED AMERICAN ALLIGATORS IN COASTAL LOUISIANA

1.1 INTRODUCTION:

The state of Louisiana manages the American alligator (*Alligator mississippiensis*) as a commercial, renewable natural resource, and management of this species through sustained use techniques is recognized as one of the best known conservation success stories in the world. The value of this resource has been conservatively estimated to be 80 to 90 million dollars annually. The majority of this value is attributed to alligators harvested from ranches which totaled 81.7 million dollars in 2014, compared to 13.8 million dollars from wild harvested individuals (Louisiana Department of Wildlife and Fisheries 2015). Beginning in 1986, Louisiana initiated a highly regulated egg collection program where licensed alligator ranchers could collect eggs from the wild, hatch them in their farms, and release a certain quota back to the wild each year from where they were originally collected. Prior to 1986, an experimental farm program was conducted where LDWF staff supplied a small number of farmers with hatchlings from state owned lands. However, the number of participants in the program increased rapidly, and it was found that allowing ranchers to collect eggs themselves from healthy, private wetlands with sustained alligator populations was more time and cost effective, and also provided an economic incentive to private landowners to manage their wetlands (Elsey et al. 1992).

Coast wide annual alligator surveys are conducted each year by Louisiana Department of Wildlife and Fisheries (LDWF) personnel to determine available alligator habitat. Once surveys are conducted, habitat availability along with nest estimates are considered and conservative egg collection quotas are set. Because natural mortality of wild hatchling alligators is high (Elsey et al. 2001), the egg collection program ensures that a portion of the population that would normally be lost survives until the juvenile stage when mortality rates are lower (Nichols et al. 1976).

Based on the sliding-scale quota, ranch-raised alligators are required to be released within two years of egg collection. This sliding scale is calculated from estimated survivorship of wild hatchlings and juveniles (Taylor and Neal 1984), with less being required to be released if the average released size is larger, and more required to be released if the average released size is smaller (Elsey et al. 2001). When the program began, LDWF required 17% of hatched alligators to be released and due to evidence of high survival of released alligators, this quota was lowered to 14% in 2000, with releases due in 2002 (Louisiana Department of Wildlife and Fisheries 2005). In 2007, the quota was again lowered from 14% to 12% with these releases due in 2009 (Louisiana Department of Wildlife and Fisheries 2008). Most recently the quota was proposed to be lowered from 12% to 10%, and if implemented with the 2017 year egg collection permits, these releases will be due in 2019 (R. M. Elsey, Louisiana Department of Wildlife and Fisheries, personal communication). Each alligator that is released is required to be between 91 and 152 cm (3 and 5 ft) in length. Before alligators are released, LDWF staff sexes, measures, and examines alligators to ensure they are healthy. Alligators are then fitted with individually numbered monel web tags, and a year specific tail scute or scutes are removed so that if tags are lost, not all information is lost with them, and year of release is still known for recaptured individuals (Elsey et al. 2001). Once recaptured, tags are recovered and individual data from each alligator is obtained for subsequent analyses.

Survival estimation of ranch-released alligators is necessary to monitor and assess the ranching program. Data to complete these analyses is obtained each year during the annual wild alligator harvest when the individually numbered monel web tags are recovered from harvested alligators. Recently, the previous modeling approach (Brownie et al. 1985, dead recovery model) estimates were noted to disagree with observed harvest data (M.D. Kaller and K.D. Capelle, unpublished report), which also was noted by Elsey et al. (1998) who suggested that a generalized linear model based approach offered a better fit. Therefore, alternative survival modeling was necessary to determine if a more appropriate approach with less disagreement between model estimates and observed data was available.

The first objective, as described in Chapter 2 of this thesis, was to implement a variety of survival models to determine which provided the best fit based on the minimization of differences between observed and predicted values. The ranching program in Louisiana depends on robust, accurate, and precise estimates of alligator survival from release to recapture. Based on this comparison of survival models, the generalized linear mixed model (GLMM) catch curve/log Leslie/age frequency model best matched model estimates with observed recaptures (which was the selected measure of modeling success), and suggested survival estimates from the GLMM were the most accurate and precise among the selected models. There is speculation that survival immediately following release is similar to high natural mortality seen in wild juvenile alligators, however, no data representing this time period is available. Therefore, the efforts in this study focused on survival modeling that began the first harvest after release. Of particular interest for these analyses was the effect of release length because of the likelihood that size at release may affect mortality (Taylor and Neal 1984). Additional objectives included exploring effects of environmental and hunter effort covariates on survival estimates as described in Chapter 3. Based on literature values and a mutli-stage Lefkovitch Matrix, Dunham et al. (2014) reported alligator viability to be influenced by temperature and precipitation and indicated that recent estimates of many population parameters were lacking in the literature. This study uses primary data to investigate those conclusions and provides modern estimates for population modeling. Alligator behaviors are known to be closely linked to temperature because of their need to thermoregulate (Joanen and McNease 1972, Terpin et al. 1979, Smith 1979, Lang 1987), and a covariate to account for temperature was included in the models. Additionally, because alligator habitat is directly influenced by precipitation [e.g. accessibility (Chabreck 1965, Joanen and McNease 1972), salinity (Chabreck 1965), and fluctuating hydrology (Brandt et al. 2016)], a covariate for precipitation was also included. The final covariate included in the models was an index of hunter effort, used to account for the effect of hunter participation on the annual harvest (Elsey et al. 1998).

Analyses suggested temperature and precipitation affect survival to harvest rates, supporting the conclusions of the literature based wild alligator model of Dunham et al. (2014). Moreover, this modeling effort added additional findings on the role of length on alligator survival. Finally, akin to the similar survival patterns observed between wild (Nichols et al. 1976, Taylor and Neal 1984) and ranch-released alligators, the similarity in response to temperature and precipitation between this study, and the findings of Dunham et al. (2014) suggest that the conclusions of this project may have some level of applicability to wild populations of alligators in Louisiana as well. Based on these results, further research into the role of environmental variables upon survival of wild alligators is warranted.

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CHAPTER 2: SELECTION OF SURVIVAL MODELS FOR COMMECRICALLY HARVESTED, RANCH-RELEASED AMERICAN ALLIGATORS

2.1 INTRODUCTION:

Unregulated harvest of the American alligator (Alligator mississippiensis) led to dramatic population declines of the species throughout its range by the 1950s. In response to the population decline, Louisiana initiated a research program on the species and closed all hunting in 1962 (Louisiana Department of Wildlife and Fisheries 2005). Five years later, in 1967, the American alligator was listed as an endangered species (Joanen and McNease 1986). From 1962 to 1972, alligators in Louisiana were totally protected. Within this time many state and federal laws were enacted to protect the species, in addition to the initiation of studies concerning a program for sustained use. During the time that alligators were protected, populations rebounded and the alligator was reclassified statewide in 1981 (Louisiana Department of Wildlife and Fisheries 2005). The reclassification returned the management authority of the species to the state of Louisiana (Joanen and McNease 1986), and the experimental sustained use program was put into effect. Through this sustained use program, Louisiana is able to manage the American alligator as a commercial, renewable natural resource. The value of this resource has been conservatively estimated to be 80 to 90 million dollars annually. The majority of this value is attributed to alligators harvested from ranches which totaled 81.7 million dollars in 2014, compared to 13.8 million dollars from wild harvested individuals (Louisiana Department of Wildlife and Fisheries 2015). Although the species is managed by the state, the export of alligator products out of the country is regulated by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The United States Fish and Wildlife Service (USFWS) regulates the CITES program and helps ensure that the harvest of threatened species is not detrimental to their survival (Louisiana Department of Wildlife and Fisheries 2005).

As a result of population declines, a research program was started in Louisiana in the 1960s to provide baseline data on alligator ecology and populations. In addition to field studies of wild alligators, captive propagation was also evaluated (Joanen and McNease 1975). Whereas it was found that alligators could successfully breed in captivity, the ranching program, started in 1986, was more time and cost effective. Prior to 1986, in addition to captive breeding, a limited number of farmers participated in an experimental farm program and were supplied hatchlings through LDWF. Due to the success of the early farming programs, the demand for hatchlings increased dramatically and could no longer be met by state personnel, leading to the development of the ranching program in place today. Through this program, licensed alligator ranchers collect eggs from the wild, hatch them in their farms, and release a certain quota back to the wild each year from where they were originally collected (Elsey et al. 1992). Coast wide annual alligator surveys are conducted each year to determine nest estimates on available alligator habitat. Once surveys are conducted, habitat availability along with nest estimates are considered and conservative egg collection quotas are set (Elsey et al. 2001). The previously set quota is required to be released within two years of hatching and is based on a sliding scale. This sliding scale is calculated from estimated survivorship of wild hatchlings and juveniles (Taylor and Neal 1984), with less being required to be released if the average released size is larger, and more required to be released if the average released size is smaller (Elsey et al. 2001). When the program began, LDWF required 17% of hatched alligators to be released and due to evidence of high survival of released alligators, this quota was lowered to 14% in 2000, with releases due in 2002 (Louisiana Department of Wildlife and Fisheries 2005). In 2007, the quota was again lowered from 14% to 12% with these releases due in 2009 (Louisiana Department of Wildlife and Fisheries 2008). Most recently the quota was proposed to be lowered from 12% to 10%, and if implemented with the 2017 year egg collection permits these releases will be due in 2019 (R. M. Elsey, Louisiana Department of Wildlife and Fisheries, personal communication). Each alligator that is released is required to be between 91 and 152 cm (3 and 5 ft) in length. Before alligators are released, LDWF staff sexes, measures, and examines alligators to ensure they are healthy. Alligators are then fitted with individually numbered monel web tags, and a year specific tail scute or scutes are removed so that if tags are lost, not all information is lost with them, and year of release is still known for recaptured individuals (Elsey et al. 2001).

Survival estimation of ranch-released alligators is necessary to monitor and assess the ranching program. The data to complete these analyses is obtained each year during the annual wild alligator harvest when the individually numbered monel web tags are recovered from harvested alligators. Recently, estimates from the previous modeling approach (Brownie et al. 1985, dead recovery model) were noted to disagree with observed harvest data. For example, the dead recovery model estimated 50% mortality for 1991 released alligators between years 2 and 3 when the observed recaptures actually increased (M.D. Kaller and K.D. Capelle, unpublished project report). Similar discrepancies were noted by Elsey et al. (1998) examining a 1990-1997 subset of the release-recapture data. Therefore, alternative survival modeling was necessary to determine if a more appropriate approach with less disagreement between model estimates and observed data was available. There are a large number of models available to analyze survival data, and these models can be generally categorized into three groups for the purpose of this study. Two model groups have extensive histories of use in wildlife, fisheries, and ecological applications. The remaining group has been more commonly applied in studies of human diseases and economics, however, have also been applied in some wildlife, fisheries, and ecological studies (e.g. bobwhite quail, Pollock et al. 1989). These categories are: 1) recreational harvest and non-exploited population models-single recapture or dead recovery models; 2) exploited population models including a traditional and Bayesian catch curve/log-Leslie/age frequency models and Beverton-Holt (1956) Length-Based model; and 3) general survival models-Cox (1972) regression; accelerated failure time models (Ridder 1990), and the Kaplan-Meier (1958) estimator (Table 2.1).

Table 2.1 List of models and their associated approaches with example species.

Model	Approach	Example Species
Recreational Harvest and Non-Exploited Population Models: Single Recapture/Dead Recovery models-Brownie, Seber, and British Trust for Ornithology Ring Recoveries (BTO)	Uses bands from dead animals, commonly used with short-lived species with high return rates (Seber 1970, Brownie et al. 1985, White and Burnham 1999). Number marked is unknown.	Mallards (*Anas platyrhynchos*) (Nichols et al. 1982), British lapwings (*Vanellus vanellus*) (Catchpole et al. 1999), Dunlin (*Calidris alpine*) (Ryan et al. 2016)
Exploited Population Models: Catch Curve (Log Leslie/Age Frequency) Models, Bayesian Catch Curve (Log Leslie/Age Structured) Models, Beverton-Holt (1956) Length-Based Model	Estimate survival of long-lived fish (Maceina 1997) and data-poor, or exploited fish populations (Chapman and Robson 1960, Thorson and Prager 2011, Millar 2014). Animals may live beyond study period.	Turtles (Order Testudines) (Shine and Iverson 1995), Bigeye tuna (*Thunnus obesus*) (Maunder and Harley 2011), Elephants (*Loxodonta africana*)(Shrader et al. 2010), Largemouth bass (*Micropterus salmoides)* (Maceina 1997)
General Survival Models: Accelerated Failure Time models, Cox (1972) Regression, Kaplan-Meier (1958) Estimator, Piecewise Regression	Estimate survival when death events are erratic or over a long period of time. Useful for staggered entry/censored data (Pollock et al. 1989). Estimate time to event with non-linear curves (Ridder 1990) with longitudinal data (Hernán et al. 2005, Zeng and Lin 2007). Animals may live beyond study period.	Bobwhite quail (*Colinus virginianus*) (Pollock et al. 1989), Wild turkey (*Meleagris gallopavo*) (Pack et al. 1999), Moose (*Alces alces*) (Testa et al. 2000), Epidemiology (Andersson et al. 2005, Hernán et al. 2005, Zeng and Lin 2007), Economics (Ridder 1990), Northern elephant seals (*Mirounga angustirostris*)(Condit et al. 2014)

Objectives of this study were to use proper model selection to determine which model(s) provided the best fit to the observed data, with the purpose of providing reliable survival estimates following release and recapture periods for ranch-released alligators in coastal Louisiana.

2.2 METHODS:

Data for these analyses were received from LDWF for the years 1991 through 2012. Data to complete the first objective of this study included number of alligators released each year, number of alligators recaptured each year, year of release, year of recapture, and sex. All data for this project comes from three, large privately held land corporations located in Vermilion and Cameron parishes in coastal Louisiana. The land corporations for this project were selected due to their large size (approximately 165,00 ha collectively), regular participation in the egg ranching program, and their history of utilizing an accessible skinning facility to process wild harvested alligators so that LDWF staff members are able to be present, maximizing tag recovery (Elsey et al. 1998). All tags for the analyses are recovered during the annual harvest that begins on the first Wednesday of September in the West zone of the state (where the three study areas are located), and lasts 30 calendar days (Louisiana Department of Wildlife and Fisheries 2015). Upon recapture, tags are recovered and information regarding individual data from release is obtained. The data used for the analyses includes only complete observations and does not include data from alligators with lost or misread tags. Male and female alligator data were separated for modeling due to differences in their biology as well as differences in catchability.

Prior to analysis several goodness of fit statistics were selected for evaluation of survival models. Because the survival models differ among parametric, semi-parametric, and non-parametric statistics and with regard to containing fixed versus random effects, selection of model fit criteria precluded many commonly used measures of model fit. The selected fit statistics were the Root Mean Square Error of Approximation (RMSEA) (Steiger 1990):

1.1 $$\mathrm{RMSEA} = \sqrt{\frac{\max\left[\frac{\mathrm{T}-\mathrm{df}}{\mathrm{N}-1}, 0\right]}{\mathrm{df}}},$$

where T is the test statistic derived from the model likelihood, df are the degrees of freedom and N is the sample size (Kim and Timm 2007), and $\hat{c}$ (Burnham and Anderson 2002):

1.2 $$\hat{c} = \frac{x^2}{\mathrm{df}},$$

where x^2 refers to the value of the chi-square statistic and df are the degrees of freedom for the model.

Because it is preferable to use simpler models that are not highly parametrized, the RMSEA (Steiger 1990) standardizes the error of approximation on the number of degrees of freedom in a model to give a measure of lack of fit (MacCallum 1995, Rigdon 1996) and to account for the complexity of the model (Hu and Bentler 2009). The $\hat{c}$ also standardizes for number of parameters in the model, and provides an estimate of over- and under-fitting of the model.

The RMSEA and $\hat{c}$ both provide measures of overall parsimonious fit, whereas other fit indices such as AIC provide measures of comparative fit (Burnham and Anderson 2002, Grace 2006). Moreover, interpretation of AIC and related fit measures (e.g. CAIC, BIC, or qAIC) in a mixed model context can be problematic (Zuur et al. 2009, Greven and Kneib 2010, Müller and Yao 2012). For these reasons, AIC was not used for model selection in these analyses. For the RMSEA an ideal fit is 0.0, values below 0.5 indicate a close fit, and any value below 0.8 is considered acceptable (Browne et al. 1993). For ĉ, an ideal fit is 1.0, therefore, the closer this value is to 1 the less over or under dispersion indicated to be present with the current model, and an adjustment for bias when computing model fit is not needed. Structural fit of the parameterized model is indicated by a value between 1 and 4 for the general linear model (Burnham and Anderson 2002) and up to 1.5, depending on model specification, for generalized linear models (Zuur et al. 2009). Gbur et al. (2012) states that ĉ values close to 1 but less than 2 indicate the GLMM is fitting well. Large values suggest that the observed variance is far greater than model predicted variance indicating that the model poorly captures the modeled process, and values less than 1 suggest that the model overfits the data and predicts more variation than observed, again indicating a poor description of the modeled process. It is important to note that if the ĉ value for a model is equal to or less than 1, the RMSEA will equal 0, and does not necessarily indicate that the model has a better fit as models with ĉ values less than 1 are considered to be overfit, as described above.

Because there are a large number of models available for survival analysis, it was important to determine which provided the best fit so that reliable survival estimates could be generated. The following sections are provided to describe the form of these models and to give a general description of the reasoning behind the selection of attempted models.

Recreational Harvest and Non-Exploited Population Models:

For all of these models, following notation in Amstrup et al. (2005), the moment estimator of survival, Si, is a solution of:

1.3 $$\frac{r_{it}}{r_{i+1,t}} = \frac{R_i \prod_{h=i}^{t-1} S_h f_i}{R_{i+1} \prod_{h=i+1}^{t-1} S_h f_i} = \frac{R_i S_i}{R_{i+1}} \ ,$$

thus,

1.4 $$\hat{S}_i = \frac{(R_{i+1} * r_{it})}{(R_i * r_{i+1,t})} \ ,$$

where R_i is the number of marked animals (usually known for the first year afield and estimated thereafter), r_{it} is the dead marked animals recaptured in a given time period (t) (this may or may not be all dead marked animals, hence the need for f_i), and f_i is the tag or mark recovery rate. The first attempted model in this category was the Brownie et al. (1985) (hereafter the Brownie dead recovery model). In the Brownie dead recovery model, S_i was estimable and the harvest related and natural components of mortality were only individually estimable as f_i (harvested and reported) and $1\text{-}S_i\text{-}f_i$ (dead from natural causes or harvested and unreported), respectively. Further, it was not possible to estimate S_i for the first and last year of the time series. Moreover, all animals in a release or tagging cohort were assumed to have the same S_i and f_i, but these estimates may vary among cohorts. The parameter r_{it} is known, f_i was not directly estimated (estimated by $1 - S_i * r_{it}$) and the parameter R_i was only known for the first year and not estimated thereafter. The second attempted model was the survival model proposed by Seber (1970), in which estimation again focused on S_i, however, the model allowed that f_i may not be estimable. Therefore, mortality ($1\text{-}S_i$) was r_{it} for reported marks and $1\text{-}r_{it}$ for all other dead animals. The final model in this category was the British Trust for Ornithology (hereafter BTO) (Catchpole et al. 1999) model that returns to the perfect case of $S_i = (R_{it}*r_{it})/(R_{i+1}*r_{i+1}))$ by assuming f_i and natural mortality are constant and allows an unknown number of released animals.

Additionally, versions of these models with 3 year, instead of single year, time steps were attempted, because longer time step models are sometimes more useful for longer lived animals (Evan Cooch, Cornell University, personal communication). All six models were implemented in PROGRAM MARK (White and Burnham 1999), and model fit statistics were derived from model likelihoods and outputs.

Exploited Population Models:

The Beverton-Holt (1956) Length Based Model, Bayesian catch curve/log Leslie/age structured models, and five catch curve/log Leslie/age frequency models were implemented as generalized linear mixed models (GLMMs). Millar (2014) reported GLMMs were a superior method to estimate mortality, which is integral to estimation of survival. Utilizing notation in Gbur et al. (2012), the GLMM was of the form:

1.5 $\quad n_{it} = \delta\left(E\left[Y_t \middle| u_1, \ldots, u_p\right]\right) = \alpha + \sum_{i=1}^{q} \beta_i x_{it} + E + \sum_{k=1}^{p} z_{kt} u_k + G, t = 1, \ldots, n$

where α represents the overall mean, β_i represents the matrix of fixed effects, x_{it} are all ith fixed effect explanatory variables on the tth observation, z_{kt} corresponds to the binary indicator variable matrix of the kth random effect, u_k, on the tth observation (Gbur et al. 2012) and δ refers to the link function that is necessary to linearize the relationship of n_{it} with β_i and z_{kt} due to overdispersion in the raw data (Breslow and Clayton 1993, Faraway 2006, Gbur et al. 2012). The response variable for this model is the number of alligators recaptured, time afield is entered as a fixed effect, and release year, accounting for the varying number of alligators released each year, is entered as a random effect. The parameter, E (added into this equation and not found in Gbur et al. (2012) notation), is the error matrix associated with n_{it} as it relates to β_i , and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014). The final parameter, G (added into this equation and not found in Gbur et al. (2012) notation), is the error matrix for n_{it} as it relates to z_{kt} (Zuur et al. 2009), and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014). The fixed effects matrix allows for direct assessment of the relationship between time afield with the number recaptured. The random effects matrix allows for inclusion of random variables or covariates that enhance the model by accounting for variation within longitudinal data but are not subject to interpretation (Dean and Nielsen 2007). Based on the 'peak' criterion, specific to catch curves (Smith et al. 2012), all modeling efforts and derived survival estimates from this data begin with data the first harvest following release, because this is the length (or age) when the majority of the alligators were subject to capture. Importantly, initial mortality associated with release is not included in this model.

All 4 GLMMs [1) fixed, Poisson; 2) random, Poisson; 3) fixed, negative binomial; and 4) random, negative binomial] were parameterized in SAS/STAT in PROC GLIMMIX (SAS Version 9.4, SAS Institute, Inc., Cary, NC). To derive survival estimates from the data, the LaPlace approximation (Wolfinger 1993, Schabenberger 2007, Gbur et al. 2012) in PROC GLIMMIX was selected as the best compromise between computation efficiency and reduced bias as compared with Guass-Hermite quadrature and penalized quasi-likelihood, respectively (Bolker et al. 2008, Gbur et al. 2012).

Three Bayesian versions of the best fitting GLMM model from the group above were constructed with informative priors for parameter estimates. A model was constructed assuming normally distributed priors for α, β_i, and z_{kt} with the negative binomial dispersion parameter prior distributed as inverse gamma. A second model was constructed assuming gamma distributed priors for α, β_i, and z_{kt} with the negative binomial dispersion parameter prior distributed as inverse gamma. A final model was constructed assuming normally distributed priors for α, β_i, and z_{kt} with the exponential dispersion parameter prior distributed as inverse gamma. For each model, 10,000 iterations were used for burn-in and 10,000 iterations were used for modeling. All Bayesian models were implemented in SAS/STAT in PROC MCMC (SAS Version 9.4, SAS Institute, Inc., Cary, NC).

A weighted catch curve (Miranda and Bettoli 2007) was also constructed based on the best fitting GLMM. Recently, Smith et al. (2012) suggested that only weighted catch curves should be used, because weighted catch curves are robust to violations of assumptions. The general structure of a weighted catch curve is:

1.6 $$\log(n_r) = \alpha + \beta_1 x_i + \varepsilon_{in},$$

1.7 $$\log(p_r) = \alpha + \beta_2 x_i + \varepsilon_{ip} .$$

In this model, the number recaptured, n_r, and time of recapture, x_i estimates a predicted number recaptured, p_r and survival as $e^{\beta 2}$. The parameters, ε_{in} and ε_{ip} are the regression error terms for the number observed and number predicted, respectively. This model was also parameterized in SAS/STAT in PROC GLIMMIX.

Instantaneous annual survival was also estimated from a length-based approach, following the method usually attributed to Beverton and Holt (1956):

1.8 $$\text{Survival} = 1 - \mathrm{K}\left(\frac{\mathrm{L}\infty - \mathrm{Lmean}}{\mathrm{Lmean} - \mathrm{Lx}}\right),$$

where L∞ is the maximum estimated size of an alligator, from a Von Bertanlanffy (1938) growth model, Lmean is the mean of the observed lengths, in this case, recapture lengths, and Lx is the minimum length harvestable. Von Bertanlanffy (1938) growth model for alligators was provided by Dr. James Geaghan, Louisiana State University Department of Experimental Statistics, and used the same data employed in survival analysis.

General Survival Models:

Cox (1972) (proportional hazards) regression is one of the most widely used of all survival models with broad application. Cox (1972) regression does not require selection of a probability distribution and associated assumptions. It should be noted that within Cox (1972) regression, a probability distribution is used to estimate the slope of the hazard (survival) function. Cox (1972) regression has other advantages including the ability to let covariates vary with time (e.g., different release numbers or lengths per year) and flexibility to incorporate discrete or continuous data. The linearized model for Cox (1972) regression is:

1.9 $$\log h_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{i2}(t) .$$

In Cox (1972) regression, the $h_i(t)$ is the hazard or risk to an individual, α(t) is the hazard at time (t), β_1 is the parameter estimate for a non-time varying explanatory variable (e.g., time afield, because the change in time between 1991 to 1992 does not vary compared with 2010 to 2011), and β_2 is the time-varying explanatory variable (e.g., different numbers of released alligators) is estimated from observed events, in this case, captures. Survival is 1- [100*(β_i-1)] for a single β_i and may be summed for the additive effect of multiple β_i. This model was also parameterized in SAS/STAT in PROC GLMMIX.

Piecewise (also break point) regression permits a model to have different slopes under alternative circumstances. Piecewise regressions are useful in survival modeling when survival rates may change over the lifetime of the animal (e.g., when juvenile survival rates may differ from adult survival rates). Following the notation in Neter et al. (1990) and Zuur et al. (2009), a piecewise regression survival model takes the form:

2.0 $$\log(n_{it}) = \alpha + B_1X_{i1} + B_2(X_{i1} - X_p)X_{i2} + E + z_{kt}u_k + G,$$

where: X_{i1} = time since release
X_{i2}=1 if $X_{i1} > X_p$
X_{i2}=0 otherwise.

In this form of piecewise regression, the solution to e^{B1} provides the estimate of survival prior to some hypothesized change point (e.g., sexual maturation, recruitment to or out of gear, etc.), X_{p2} and the solution to e^{B2} estimates survival after the change point. As above, the parameter,E, is the error matrix associated with n_{it} as it relates to X_i, and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014). The parameters, z_{kt} and u_k are the slope of the random effects (as a column matrix or vextor), in this case the number of alligators released. The final parameter G, is the error matrix for n_{it} as it relates to $z_{kt}u_k$ (Zuur et al. 2009), and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014).This model was parameterized in SAS/STAT in PROC NLMIXED (SAS Version 9.4, SAS Institute, Inc., Cary, NC).

Accelerated Failure Time (or Rate) models (hereafter AFT) are a parametric model class that analyzes the relationship between survivor functions between individuals (Ridder 1990). These models are designed to identify variables that are linked to differences in survival among individuals (e.g., number released at the same time, and year of release). As parametric models, probability distributions must be selected. Each probability distribution is a compromise among flexibility to fit the observed data, data requirements, and computational difficulty. The general form of the model is:

2.1 $$S(t_i) = S_i(\theta_{ij} * t_i).$$

In these models, θ_{ij} is a constant specific to the data, t_i is the year since release, and S_i is the survivorship function, which is selectable from the available probability distributions.

The model also may be written as:

2.2 $$\log(T_i) = \alpha + \beta_1 x_1 + \sigma\varepsilon_i.$$

In this case, T_i is the random variable representing the time until an event (e.g., capture) for an individual and α, β_1, and σ are typical regression parameters for the intercept, slope of the x_1, and the variance. The parameter, ε is determined by the selected probability distribution, which determines the survival estimate. For log normal models, survival is $100*(e^{\beta i}-1)$. For the exponential model, survival is $e^{\beta i}$. For the log-logistic, Weibull, and gamma models, survival is $e^{\beta i/scale}$. All versions, log normal, log-logistic, Weibull, gamma, and exponential models were parameterized in SAS/STAT in PROC LIFEREG (SAS Version 9.4, SAS Institute, Inc., Cary, NC).

The Kaplan-Meir (1958) estimator is non-parametric. Survival is modeled as:

2.3 $$S(t) = \prod_{t_i<t} \frac{n_i - d_i}{n_i}.$$

Kaplan-Meir (1958) estimator requires n_i to be the number of animals alive just before death, d_i is the number of death (or captures), and t are times. The estimator allows for right censoring for any reason, which may be beneficial in situations of unknown mortality. This model was parameterized in SAS/STAT in PROC LIFETEST (SAS Version 9.4, SAS Institute, Inc., Cary, NC).

2.3 RESULTS:

Of the 23 models evaluated for model fit, the best fitting models were variations of the generalized linear mixed model (GLMM) catch curve (Table 2.2). The best fitting model had $\hat{c}$ values of 0.88 for female alligators and 1.0 for male alligators, indicating minimal overdispersion with the selected negative binomial probability distribution. Because the $\hat{c}$ values were ≤ 1, the best fitting model had a RMSEA value of 0.00 for male and female alligators, indicating good fit to the data in combination with suitable $\hat{c}$ values (Hu and Bentler 1999). Overall, catch curves/log Leslie/age structured model group fit the data better than recreational harvest models and the more general survival models. The Beverton-Holt (1956) length based model provided a single point estimator for female (0.85) and male (0.84) data, thus, could not be evaluated in the same manner.

Table 2.2. Results of model fitting ordered from best to worst fit, and corresponding fit statistics.

Model	Mean Annual Estimate of Survival (all)	Mean Annual Estimate of Survival (male)	Mean Annual Estimate of Survival (female)	X^2 Fit Statistic ($\hat{c}$) (females/males) Fit = 1.0	RMSEA Fit Statistic (females/males) smaller is better
Generalized Linear Mixed Model Catch Curve – fixed intercept, negative binomial	0.88	0.87	0.89	0.88/1.0	0.00/0.00
Generalized Linear Mixed Model Catch Curve – random intercept, negative binomial	0.89	0.87	0.89	0.88/1.0	0.00/0.00
Generalized Linear Mixed Model Catch Curve – fixed intercept, Poisson	0.94	0.94	0.95	0.43/0.52	0.00/0.00
Generalized Linear Mixed Model Catch Curve – random intercept, Poisson	0.94	0.93	0.95	0.43/0.52	0.00/0.00
Weighted Catch Curve	0.89	0.88	0.90	0.36/0.31	0.00/0.00
Bayesian Mixed Model Catch Curve – fixed intercept, negative binomial, normal priors	0.79	0.80	0.79	2.10/2.51	0.09/0.07
Bayesian Mixed Model Catch Curve – fixed intercept, negative binomial, gamma priors	0.79	0.79	0.79	2.10/2.51	0.09/0.07
Bayesian Mixed Model Catch Curve – fixed intercept, negative binomial, exponential priors	0.79	0.79	0.79	2.10/2.51	0.09/0.07
Piecewise Regression	0.84	0.83	0.84	5.38/4.96	0.15/0.14
BTO	0.78	0.78	0.79	8.66 *	0.41*
Brownie et al. (1985)	0.95	0.90	0.96	11.75 *	0.48*
Seber (1970)	0.95	0.94	0.95	11.76 *	0.48*
Accelerated Failure Time (log logistic)	0.81	0.81	0.81	449/429	0.90/0.88
Accelerated Failure Time (lognormal)	0.99	0.99	0.99	460/475	0.92/0.93
Accelerated Failure Time (Weibull)	0.83	0.83	0.83	484/501	0.94/0.96
Accelerated Failure Time (gamma)	0.87	0.83	0.88	493/482	0.95/0.94
Accelerated Failure Time (exponential)	0.99	0.99	0.99	546/534	1.0/0.99
Kaplan-Meier Estimator	0.47	0.46	0.47	524/1024	0.99/1.39
Cox Regression	0.51	0.47	0.52	2082/1411	1.94/1.60
Seber – 3 yr increments	0.91	0.90	0.93	61.4*	2.75*
BTO – 3 yr increments	0.61	0.57	0.64	65.0*	2.83*
Brownie – 3 yr increments	0.92	0.90	0.95	76.27*	3.27*

*combined male and female data, estimated from likelihoods

The GLMM catch curve, negative binomial probability distribution, with a random intercept fit just as well as the GLMM catch curve, negative binomial distribution, with a fixed intercept that was selected as the best fitting model. However, because a survival estimate of specific years was not of interest, and, instead, the interest was in mean annual survival, the fixed intercept version was selected. In addition, the fixed intercept version is more parsimonious as it uses fewer degrees of freedom and is thus a mathematically simpler method to estimate the survival parameter (Schabenberger 2005).

The GLMM catch curve with a Poisson distribution, with fixed and random intercepts, were the third and fourth best fitting models, respectively. However, because overdispersion was present in the data, the Poisson distribution was unable to account for the increased variance associated with longitudinal count data, and led to the poor fit of these models (Gbur et al. 2012). The weighted catch curve, which is used to account for the impact of outlying, older individuals in the data by assigning these observations a lesser weight than individuals that occur more often (Maceina and Betolli 1998, Miranda and Bettoli 2007), had the poorest fit of the catch curve group. Finally, the three Bayesian implementations of the catch curve models fit the data less well than non-Bayesian counterparts suggesting the incorporation of priors did not enhance the precision estimates, in this case.

As expected, the fit of the additional attempted models are closely ordered into their respective groups, with the exception of piecewise regression, which exhibited better fit than the recreational harvest models. The recreational harvest and non-exploited population models, including BTO, Brownie dead recovery, and Seber (1970) exhibit close fit, with the BTO underestimating survival and the latter two models overestimating survival. The more general survival models commonly used with censored data, AFT, Kaplan-Meier (1958) estimator and Cox (1972) regression are all closely grouped with similar poor fits. The AFT models however, tend to overestimate survival, whereas the Kaplan-Meier estimator and Cox (1972) regression appear to underestimate survival. The last three models listed are a variation of the recreational harvest models attempting to estimate survival in 3 year increments as opposed to every year. Although the survival estimates of the attempted models are briefly mentioned here, it is unwise to assign any real meaning to these estimates as the fit of the models are poor.

The best fitting female model, the GLMM catch curve with a fixed intercept and, negative binomial distribution, estimated instantaneous annual survival to be 0.87 for males and 0.89 for females. Survival estimates from each model are given in the form of instantaneous annual survival. In this context, the GLMM catch curve models provide the predicted number of recaptures given the explanatory variables (in this case, time afield). This approach is analogous to the interpretation of survival by Ricker (1944) from the slope of the exponential relationship between number recaptured with time. However, in the GLMM context rather than interpreting a single slope parameter, the entire model of explanatory variables and covariates are simultaneously interpreted as an estimate of survival. The advantage of this interpretation is the contribution of each explanatory variable or covariate can thus be partitioned into components of the GLMM. Converting instantaneous annual survival to annual survival can be achieved using exponentiation. The formula to estimate survival is:

2.4 $$z = e^{\alpha + B_1 X_1 + \cdots + B_p X_p},$$

thus,

2.5 $$\hat{S}_i = z^{\text{year of interest}},$$

where z is the estimate of instantaneous annual survival and Si is the estimated annual survival rate. The linear predictor for the model of interest is represented by $\alpha + B_1 X_1 + \cdots + B_p X_p$ where α is the intercept, and $B_p X_p$ refers to the combinations of covariates and their corresponding coefficients. Each X_p refers to the value of the mean for the explanatory variable or covariate it represents. By solving for the linear predictor and using exponentiation, instantaneous annual survival (z) can be estimated. To estimate survival for any other year the value of instantaneous annual survival, z, is raised to the year of interest to provide an estimate of annual survival (S_i). For example, if survival during year 10 was desired, z^{10} would provide that estimate.

Table 2.3. Estimated annual survival by year from the best fitting model with 95% confidence intervals. These estimates are for any given year and fully adjusted for inter-annual variation.

Years Since Release	Survival (female)	Lower 95%	Upper 95%	Survival (male)	Lower 95%	Upper 95%
1	0.89	0.87	0.91	0.87	0.85	0.90
2	0.79	0.75	0.83	0.76	0.73	0.81
3	0.70	0.65	0.75	0.66	0.62	0.72
4	0.63	0.56	0.68	0.57	0.53	0.65
5	0.56	0.49	0.62	0.50	0.45	0.58
6	0.50	0.42	0.56	0.43	0.38	0.52
7	0.44	0.37	0.51	0.38	0.33	0.47
8	0.39	0.32	0.46	0.33	0.28	0.42
9	0.35	0.28	0.42	0.29	0.24	0.38
10	0.31	0.24	0.38	0.25	0.20	0.34
11	0.28	0.21	0.35	0.22	0.17	0.30
12	0.25	0.18	0.32	0.19	0.15	0.27
13	0.22	0.16	0.29	0.16	0.13	0.24
14	0.20	0.13	0.26	0.14	0.11	0.22
15	0.17	0.12	0.24	0.12	0.09	0.20
16	0.15	0.10	0.22	0.11	0.08	0.18
17	0.14	0.09	0.20	0.09	0.07	0.16
18	0.12	0.08	0.18	0.08	0.06	0.14
19	0.11	0.07	0.16	0.07	0.05	0.13
20	0.10	0.06	0.15	0.06	0.04	0.11
21	0.09	0.05	0.13	0.05	0.03	0.10
22	0.08	0.04	0.12	0.05	0.03	0.09
23	0.06	0.04	0.11	0.04	0.02	0.08

The following figures provide a representation of the data used in these analyses, including, raw data (Figures 2.1 and 2.2) for male and female alligators as well as the same data after log transformation (Figures 2.3 and 2.4).

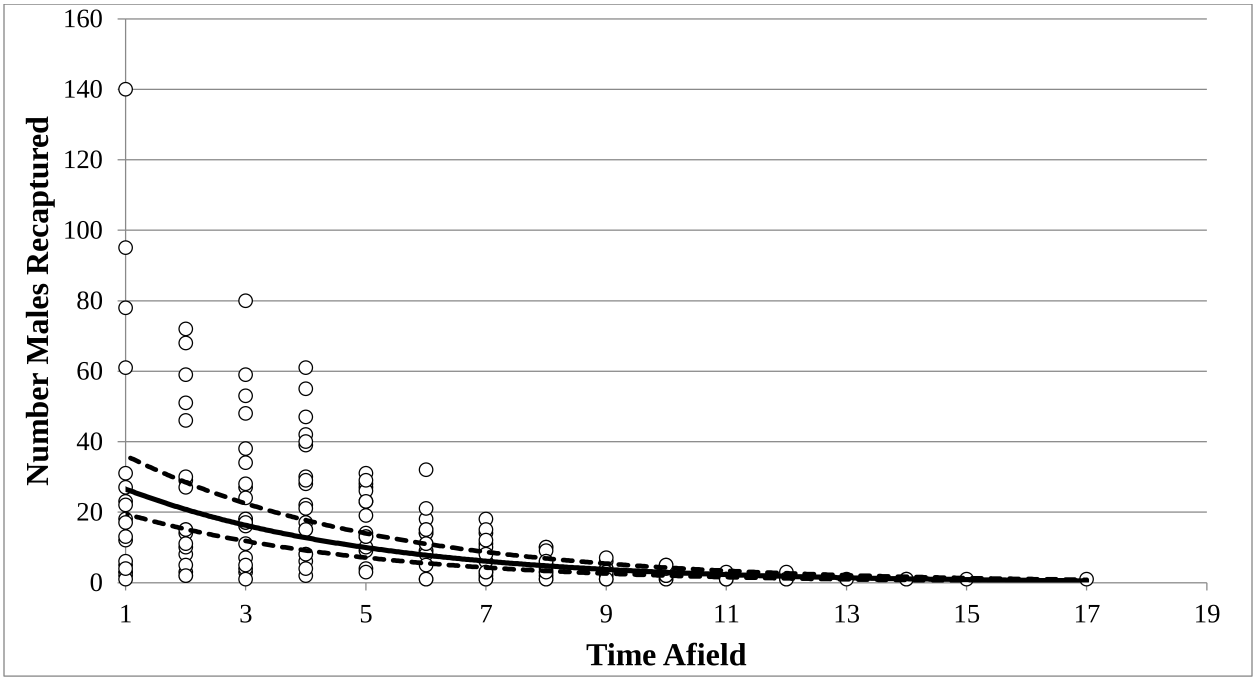

Figure 2.1. Relationship between observed number of males recaptured and time afield. Circles represent observed recaptured males, whereas the solid line is model estimated number of recaptures. Dotted lines represent 95% confidence intervals.

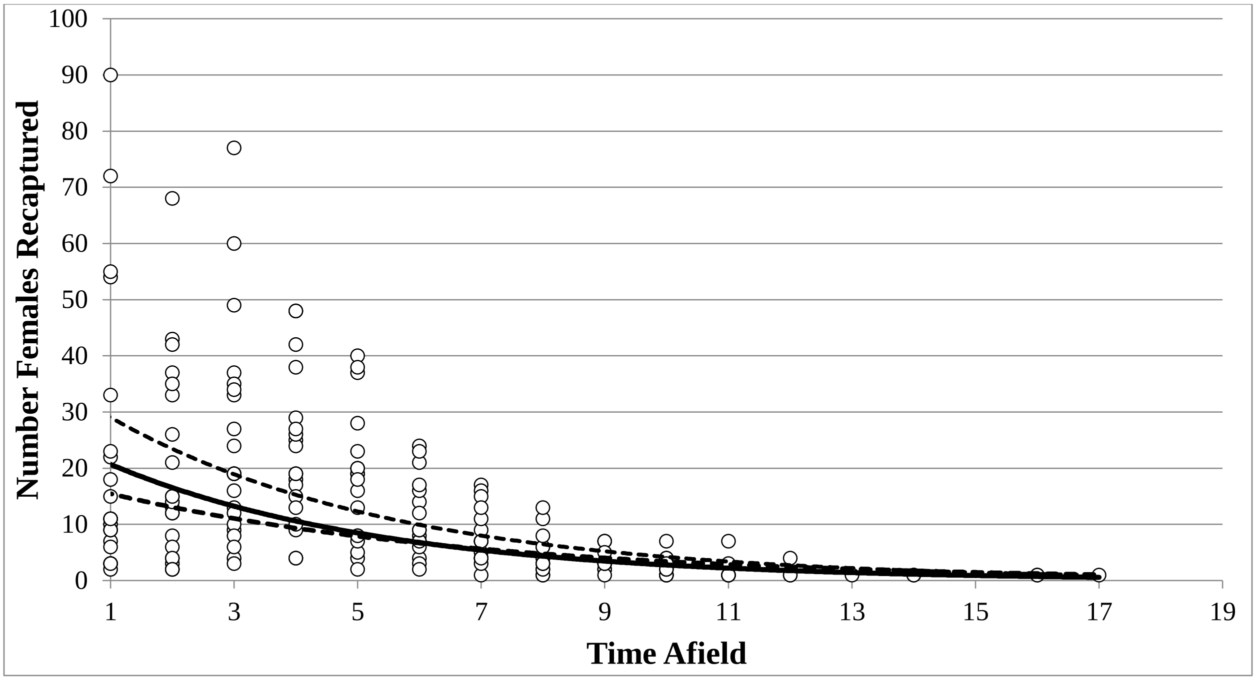

Figure 2.2. Relationship between observed number of females recaptured and time afield. Circles represent observed recaptured females, whereas the solid line is the model estimated number of recaptures. Dotted lines represent 95% confidence intervals.

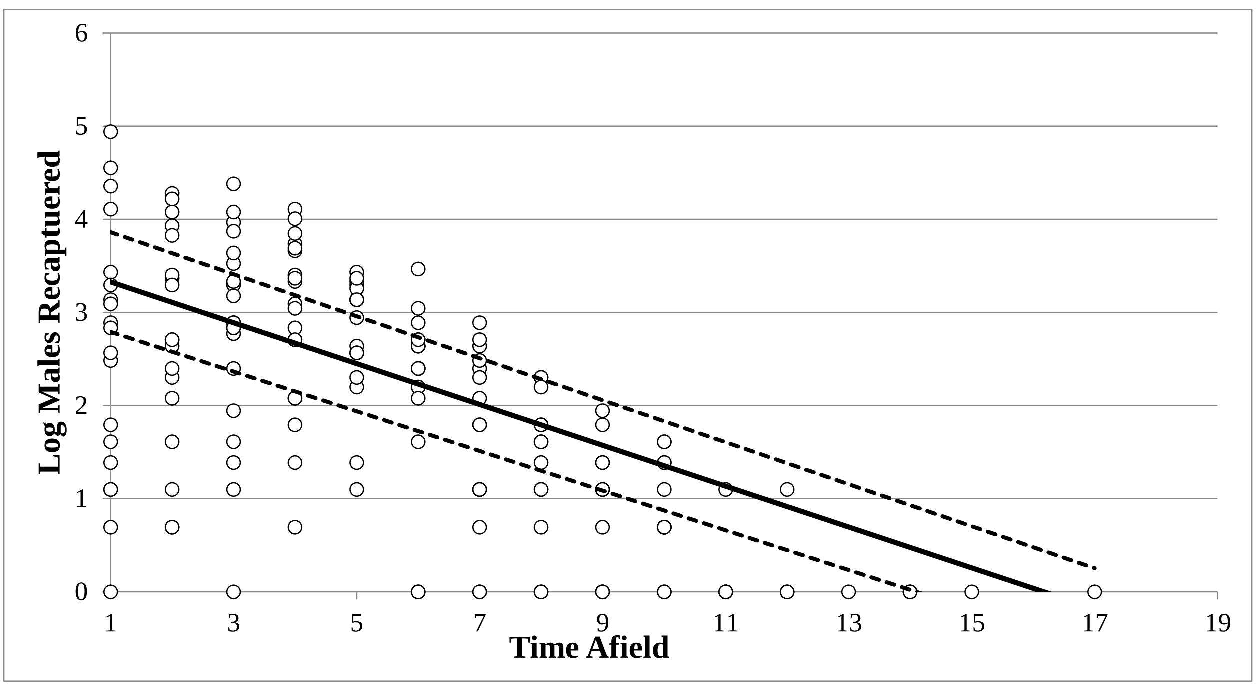

Figure 2.3. Relationship between observed log number of males recaptured and time afield. Circles represent observed log of recaptured males, whereas the solid line is the model estimated log number of recaptures. Dotted lines represent 95% confidence intervals.

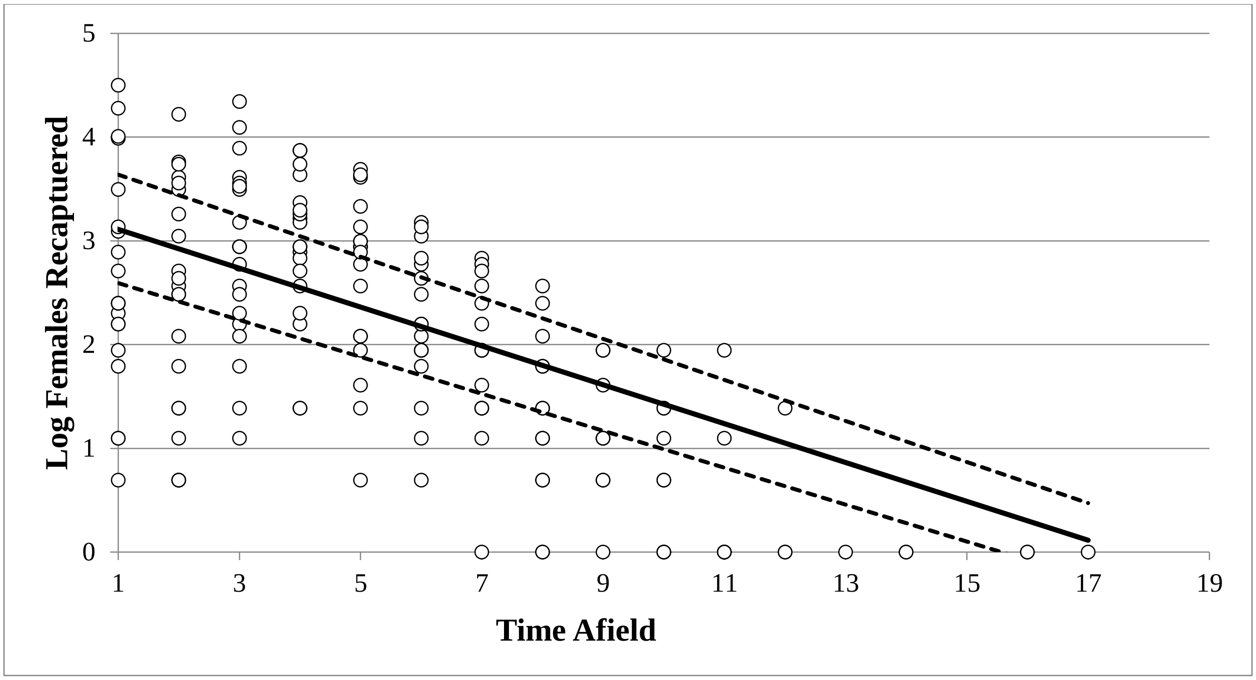

Figure 2.4. Relationship between observed log number of females recaptured and time afield. Circles represent observed log of recaptured females, whereas the solid line is the model estimated log number of recaptures. Dotted lines represent 95% confidence intervals.

2.4 DISCUSSION:

Whereas each category of survival models has advantages, violations of the assumptions associated with each model presumably led to poor fits for most of the attempted models, and unreliable survival estimates for ranch-released alligators following the first harvest period (Table 2.2). However, from the set of exploited population models, the pair of catch curve/log Leslie/age structured models based on GLMMs with a negative binomial probability distribution and fixed and random intercepts did exhibit good model fit. These models have been proposed for use in exploited fisheries as a replacement for linear regression based methods (Millar 2014). Because close fit between model predicted recaptures and observed recaptures was the selected measure of success, these models, specifically the fixed intercept from, would be the recommended models for ranch-released alligator survival estimation.

Recreational Harvest and Non-Exploited Population Models:

Recreational harvest and non-exploited population models most likely were not appropriate for this data because of mismatches between the model structures and assumptions with available data. For example, the recovery data matrix generally used with the Brownie et al. (1985) dead recovery model shows a high number of recoveries in the year immediately following tagging (Rodriguez-Marin et al. 2005), whereas, for the alligator data matrix, this is not the case. In addition, the assumption of the Brownie dead recovery model that all tagged individuals have the same recovery probability (Brownie et al. 1985) may not be appropriate for this dataset, as large alligators are more valuable and thus harvest techniques biased against smaller alligators are often used (Elsey et al. 1998). Elsey et al. (1998) also noted that the Brownie et al. (1985) dead recovery model poorly fit a subset of 1990-1997 alligator recapture data, however, the authors did not achieve a much better fit with a minimum-known-alive generalized linear model (logit link, binomial distribution) suggesting that size-selective harvest practices may have violated model assumptions in both cases. Another reason for the poor fit of the Brownie dead recovery model may be the parameterization of the model which requires separating natural and harvest mortality, a step that may not be necessary with adult alligator survival data. Alligators are a long-lived (Chabreck and Joanen 1979), top predator (Delany and Abercrombie 1986) likely to experience low natural mortality among mature individuals (Taylor and Neal 1984). With recaptures of some individuals in this dataset over 20 years, it is likely that very few natural age-based mortality events are occurring. The Brownie dead recovery model also takes into account differences in reporting rates (Brownie et al. 1985) but because alligator harvest for areas included in this study are strictly regulated and conducted where the assurance of tag recovery is likely, this also may not be a factor.

Although similar, the Seber (1970) model has slightly different assumptions than the Brownie dead recovery model. The Seber (1970) model relaxes the assumption of separating natural and harvest induced mortality, and does not take into account reporting rates. Despite relaxed assumptions, the model fit poorly, which may have been related to the problems of the Seber model producing confidence intervals when parameter estimates are near the boundaries (White and Burnham 1999), as appears to be the case with the alligator data (i.e., 0.88 combined survival is near the 1.0 parameter boundary).

The BTO model is commonly used when the number of tagged individuals is not known (Catchpole et al. 1999). This model is limited in its abilities due to this assumption, and is unfit to handle the format of observations for the alligator dataset, resulting in poor fit.

General Survival Models:

The Cox (1972) regression model, AFT, and Kaplan-Meier (1958) estimator, are flexible models commonly used with censored data. The Cox (1972) regression model likely failed because of the failure of the specified hazard function to converge for the time dependent covariates included in the model (Yamaguchi 1992, Hess 1995). In addition, Cox (1972) regression requires that the proportional hazard is the same among groups (Orbe et al. 2002), an assumption that may not be true for released cohorts in the alligator analysis.

The AFT model is very similar to the Cox (1972) regression with the differences between the models lying in the probability distribution of the hazard function. Cox (1972) regression is semi-parametric and requires no assumptions about the survival time, whereas the AFT models are parametric and require a selected probability distribution (Gutierrez 2002). The failure of the

AFT models to fit the alligator data set are likely due to violations associated with the shape of the selected probability distributions (Orbe et al. 2002).

The Kaplan-Meier (1958) estimator is a non-parametric approach, similar to the Cox (1972) and AFT models, but fails when the underlying survival function follows a simple survival curve such as the exponential curve of the released alligators. This is because the Kaplan-Meier (1958) survival curve requires more parameters than a simple curve uses, and thus defies the rule of parsimony (Pollock et al. 1989).

Exploited Population Models:

Catch curves have been used for the analysis of mortality associated with fisheries for many years using the general and generalized linear model framework. However, Millar (2014) introduced catch curves in the framework of the GLMM, allowing for annual variation in recruitment by use of random variables. This method results in more accurate and precise survival estimates, and the modeling of alligator data clearly selected GLMM catch curves as the best fitting models for survival data. The limitation of this model is that survival must be assumed to be constant across release cohorts (Chapman and Robson 1960), except where covariate information (e.g., time afield) can modify survival estimates (Smith et al. 2012). Even with this limitation, the model fits and provides information on expected survival rates, estimates of alligators surviving to given points in time, and a framework to include variables and covariates of interest, such as release length. Although often used with fish species, the alligator program in Louisiana is managed much like a fishery and is perhaps the reason for the exceptional fit of this class of models.

2.5 SUMMARY:

The ranch-released American alligator program in Louisiana depends on robust, accurate, and precise estimates of alligator survival from release to recapture. Based on this comparison of survival models, the GLMM catch curve/log Leslie/age frequency model best matched model estimated with observed recaptures, which was the selected measure of modeling success, suggesting that survival estimates from the GLMM were the most accurate and precise among the selected models. GLMMs are well demonstrated to be more precise and more robust than other similar models (Millar 2014). Importantly, survival estimates in this study were somewhat higher than survival estimates of wild Louisiana male [77.5% wild, Nichols et al. (1976), Taylor and Neal (1984) vs. 87% ranch-released, this study] and wild female Louisiana alligators [79% wild, Nichols et al. (1976), Taylor and Neal (1984) vs. 89% ranch-released, this study], which may represent different environmental conditions in coastal Louisiana, potential inherent differences between wild and ranch-released alligators (e.g., larger size-at-age of ranch-released alligators, accelerated growth), or changes in harvest and regulatory practices between the 1970s with the 1990-2010s. Alternatively, estimated survival differences may not have been biological or regulatory and may have been the result of modeling technological improvements (i.e., GLMMs) and a better match between available data and model assumptions. Importantly, it should be noted that Taylor and Neal (1984) were estimating all mortality and hence, their estimates included environmental variation and other factors not modeled in this chapter. This chapter only estimated survival to harvest based on harvest data excluding these elements. In summary, a GLMM based approach to modeling ranch-released alligator survival provided the best available survival estimates for alligator management in Louisiana.

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CHAPTER 3: USING GENERALIZED LINEAR MIXED MODELS TO EVALUATE THE SURVIVAL OF RANCH-RELEASED, COMMERCIALLY HARVESTED AMERICAN ALLIGATORS IN COASTAL LOUISIANA

3.1 INTRODUCTION:

The state of Louisiana manages the American alligator (*Alligator mississippiensis*) as a commercial, renewable natural resource, and management of this species through sustained use techniques is recognized as one of the best known conservation success stories in the world. The value of this resource has been conservatively estimated to be 80 to 90 million dollars annually. The majority of this value is attributed to alligators harvested from ranches which totaled 81.7 million dollars in 2014, compared to 13.8 million dollars from wild harvested individuals (Louisiana Department of Wildlife and Fisheries 2015). Beginning in 1986, Louisiana initiated a highly regulated egg collection program where licensed alligator ranchers could collect eggs from the wild, hatch them in their farms, and release a certain quota back to the wild each year from where they were originally collected. Prior to 1986, an experimental farm program was conducted where LDWF supplied a small number of farmers with hatchlings from state owned lands. However, the number of participants in the program increased rapidly, and it was found that allowing ranchers to collect eggs themselves from healthy, private wetlands with sustained alligator populations was more time and cost effective, and additionally provided an economic incentive to private landowners to manage their wetlands (Elsey et al. 1992).

Coast wide annual alligator surveys are conducted each year by Louisiana Department of Wildlife and Fisheries (LDWF) personnel to determine available alligator habitat. Once surveys are conducted, habitat availability along with nest estimates are considered and conservative egg collection quotas are set. Because natural mortality of wild hatchling alligators is high (Elsey et al. 2001), the egg collection program ensures that a portion of the population that would normally be lost, survives until the juvenile stage when mortality rates are lower (Nichols et al. 1976).

Based on the quota, ranch-raised alligators are required to be released within two years of egg collection, which is based on a sliding scale. This sliding scale is calculated from estimated survivorship of wild hatchlings and juveniles (Taylor and Neal 1984), with less being required to be released if the average released size is larger, and more required to be released if the average released size is smaller (Elsey et al. 2001). When the program began, LDWF required 17% of hatched alligators to be released and due to evidence of high survival of released alligators, this quota was lowered to 14% in 2000, with releases due in 2002 (Louisiana Department of Wildlife and Fisheries 2005). In 2007, the quota was again lowered from 14% to 12% with these releases due in 2009 (Louisiana Department of Wildlife and Fisheries 2008). Most recently the quota was proposed to be lowered from 12% to 10%, and if implemented with the 2017 year egg collection permits these releases will be due in 2019 (R. M. Elsey, Louisiana Department of Wildlife and Fisheries, personal communication). Each alligator that is released is required to be between 91 and 152 cm (3 and 5 ft) in length. Before alligators are released, LDWF staff sexes, measures, and examines alligators to ensure they are healthy. Alligators are then fitted with individually numbered monel web tags, and a year specific tail scute or scutes are removed so that if tags are lost, not all information is lost with them, and year of release is still known for recaptured individuals (Elsey et al. 2001). Once recaptured, tags are recovered and individual data from each alligator is obtained for subsequent analyses.

The main objective of this study was to evaluate the survival to harvest of the ranch-released alligators based upon information from web tags that were recovered during the annual harvest from the years 1991 to 2014, for the purpose of providing survival estimates following the first year to potentially refine management recommendations. There is speculation that the survival immediately following release is similar to high natural mortality seen in wild juvenile alligators, however, no data representing this time period is available. Therefore, the efforts in this chapter focused on survival modeling that began the first harvest after release. Of particular interest for these analyses was the effect of release length because of the knowledge that size at release may affect mortality (Taylor and Neal 1984). Additional objectives included exploring the effects of environmental and hunter effort covariates. Based on literature values and a mutli-stage Lefkovitch Matrix, Dunham et al. (2014) reported alligator viability to be influenced by temperature and precipitation and indicated that recent estimates of many population parameters were lacking in the literature. This study uses primary data to investigate those conclusions and provides modern estimates for population modeling. Alligator behaviors are known to be closely linked to temperature because of their need to thermoregulate (Joanen and McNease 1972, Terpin et al. 1979, Smith 1979, Lang 1987), and a covariate to account for temperature was included in the models. Additionally, because alligator habitat is directly influenced by precipitation [e.g. accessibility (Chabreck 1965, Joanen and McNease 1972), salinity (Chabreck 1965), and fluctuating hydrology (Brandt et al. 2016)], a covariate for precipitation was also included. The final covariate included in the models was an index of hunter effort, used to account for the effect of hunter participation on the annual harvest (Elsey et al. 1998).

3.2 METHODS:

Data for these analyses were received from LDWF for the years 1991 through 2014. Data for this chapter included number of alligators released each year, number of alligators recaptured each year, year of release, year of recapture, length at release, length at recapture, and sex. All data for this project comes from three, large privately held land corporations located in

Vermilion and Cameron parishes in coastal Louisiana. The land corporations for this project were selected due to their large size (approximately 165,00 ha collectively), regular participation in the egg ranching program, and their history of utilizing an accessible skinning facility to process wild harvested alligators so that LDWF staff members are able to be present, maximizing tag recovery (Elsey et al. 1998). All tags for the analyses are recovered during the annual harvest that begins on the first Wednesday of September in the West zone of the state (where the three study areas are located), and lasts 30 calendar days (Louisiana Department of Wildlife and Fisheries 2015). Upon recapture, tags are recovered and information regarding individual data from release is obtained. The data used for the analyses includes only complete observations and does not include data from alligators with lost or misread tags. Male and female alligator data were separated for modeling due to differences in their biology as well as differences in catchability.

Prior to analysis several goodness of fit statistics were selected for evaluation of survival models. The selected fit statistics were the Root Mean Square Error of Approximation (RMSEA) (Steiger 1990):

1.1 $$\mathrm{RMSEA} = \sqrt{\frac{\max\left[\frac{T-df}{N-1},0\right]}{df}},$$

where T is the test statistic derived from the model likelihood, df are the degrees of freedom and N is the sample size (Kim and Timm 2007), and $\hat{c}$ (Burnham and Anderson 2002):

1.2 $$\hat{c} = \frac{x^2}{df},$$

where x^2 refers to the value of the chi-square statistic and df are the degrees of freedom for the model. Nagelkerke's R^2(1991) was selected as a third, exploratory way to assess model fit, as it compares the prediction ability of the current model relative to the intercept only or null model (Tjur 2009). Although R^2 approaches are not traditionally associated with generalized linear mixed models (McCullagh and Nelder 1989), Nagelkerke R^2 (1991) is an appropriate option for these models (Tjur 2009) and its implementation followed Jónsson et al. (2016).

Because it is preferable to use simpler models that are not highly parametrized, the RMSEA (Steiger 1990) standardizes the error of approximation on the number of degrees of freedom in a model to give a measure of lack of fit (MacCallum 1995, Rigdon 1996) and to account for the complexity of the model (Hu and Bentler 1999). The $\hat{c}$ also standardizes for number of parameters in the model, and provides an estimate of over- and under- fitting of the model.

The RMSEA and $\hat{c}$ both provide measures of overall parsimonious fit, whereas other fit indices such as AIC, provide measures of comparative fit (Burnham and Anderson 2002, Grace 2006). Moreover, interpretation of AIC and related fit measures (e.g. CAIC, BIC, or qAIC) in a mixed model context can be problematic (Zuur et al. 2009, Greven and Kneib 2010, Müller et al. 2012). For these reasons, AIC was not used for model selection in these analyses. For the RMSEA an ideal fit is 0.0, values below 0.5 indicate a close fit, and any value below 0.8 is considered acceptable (Browne et al. 1993). For $\hat{c}$, an ideal fit is 1.0, therefore, the closer this value is to 1, the less over or under dispersion indicated to be present with the current model, and an adjustment for bias when computing model fit is not needed. Structural fit of the parameterized model is indicated by a value between 1 and 4 for the general linear model (Burnham and Anderson 2002) and up to 1.5, depending on model specification, for generalized linear models (Zuur et al. 2009). Gbur et al. (2012) states that $\hat{c}$ values close to 1 but less than 2 indicate the GLMM is fitting well. Large values suggest that the observed variance is far greater than model predicted variance indicating that the model poorly captures the modeled process, and values less than 1 suggest that the model overfits the data and predicts more variation than observed, again indicating a poor description of the modeled process. It is important to note that if the $\hat{c}$ value for a model is equal to or less than 1, the RMSEA will equal 0, and does not necessarily indicate that the model has a better fit as models with $\hat{c}$ values less than 1 are considered to be overfit, as described above. The higher the value of Nagelkerke's R^2 (1991), up to 1.0, the higher the predictive power of the current model.

The fixed intercept generalized linear mixed model (GLMM) catch curve, was selected to model the survival of the ranch-released alligators (Chapter 2), and utilizing notation in Gbur et al. (2012) was of the form:

1.3 $\quad n_{it} = \delta\left(E\left[Y_t \middle| u_1, \dots, u_p\right]\right) = \alpha + \sum_{i=1}^{q} \beta_i x_{it} + E + \sum_{k=1}^{p} z_{kt} u_k + G, t = 1, \dots, n$

where α represents the overall mean, β_i represents the matrix of fixed effects, x_{it} are all ith fixed effect explanatory variables on the tth observation, z_{kt} corresponds to the binary indicator variable matrix of the kth random effect, u_k, on the tth observation (Gbur et al. 2012) and δ refers to the link function that is necessary to linearize the relationship of n_{it} with β_i and z_{kt} due to overdispersion in the raw data (Breslow and Clayton 1993, Faraway 2006, Gbur et al. 2012). The response variable for this model is the number of alligators recaptured. The parameter, E (added into this equation and not found in Gbur et al. (2012) notation), is the error matrix associated with n_{it} as it relates to β_i and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014). The final parameter, G (added into this equation and not found in Gbur et al. (2012) notation), is the error matrix for n_{it} as it relates to z_{kt} (Zuur et al. 2009), and was specified to follow the negative binomial and Poisson probability distributions (Lawless 1987, Millar 2014). The fixed effects matrix allows for direct assessment of the relationship between all fixed effects with the number recaptured. The random effects matrix allows for inclusion of random variables or covariates that enhance the model by accounting for variation within longitudinal data but are not subject to interpretation (Dean and Nielsen 2007). Based on the 'peak' criterion, specific to catch curves (Smith et al. 2012), all modeling efforts and derived survival estimates from this data begin with data the first harvest following release, because this is the length (or age) when the majority of the alligators were subject to capture. Importantly, initial mortality associated with release is not included in this model.

Once the best fitting model was selected, individual lengths were incorporated as fixed effects, along with additional covariates of interest, also added as fixed effects. Average annual values of market prices (used as an index of hunter effort and hereafter referred to as index of hunter effort), temperature, and precipitation, along with a measure of variability for each of the climate variables (hereafter referred to as coefficient of variation or cv) (Mearns et al. 1997), were incorporated into survival models to determine if model fit improved with their addition, and if the covariates were statistically significant (Table 3.1). Release year was again used as a random variable, to account for interval censoring in these models (Millar 2014).

Table 3.1. List of generalized linear mixed model covariates and justifications for each covariate.

Included Variables and Covariates	Justification
Release Length	Knowledge that size at release affects alligator survival (Taylor and Neal 1984)
Recapture Length	Larger alligators are more valuable and hunters use methods to target larger alligators (Elsey et al. 1998)
Precipitation and Temperature Means	Unfavorable climate conditions (e.g. severe drought) led to lowered quotas in some years (Elsey et al. 1998). Identified by population model (Dunham et al. 2014)

(Table 3.1 Continued)

Included Variables and Covariates	Justification
Coefficient of Variation for Precipitation and Temperature	Variability in climate may affect behavior (Joanen and McNease 1972) which could influence survival. Identified by population model (Dunham et al. 2014)
Index of Hunter Effort	If prices are high, hunters may be selective toward larger alligators resulting in fewer recaptures of tagged alligators (Elsey et al. 1998)

Additionally, because environmental conditions and market prices in prior years to recapture could influence survival (i.e., have inherent temporal autocorrelation or trends), ARIMA (autoregressive integrated moving average) models were constructed to examine temporal correlation between recapture and survival estimates with 20 previous years data and determined statistical significance, if any, by incorporating the previous conditions into survival models (Cryer and Chan 2008). All climate variables were added to data associated with year of release, and year of recapture to determine which previous years climate variables were more influential for alligator survival. ARIMA models were implemented in PROC ARIMA in SAS/STAT (SAS Version 9.4, SAS Institute, Inc., Cary, NC).

For both GLMM and ARIMA models, climate data was obtained from the National Centers for Environmental Information (NCEI) through the National Oceanic and Atmospheric Administration (NOAA) and was available in monthly formats for the study area by parish. Market prices were obtained from ‘Louisiana Alligator Management Program, Annual Report 2014-2015’. An annual mean was calculated for each climate and market (index of hunter effort) covariate. The annual mean and coefficient of variation (cv) for temperature included only months with an average temperature above 16°C because alligators are often dormant, and do not eat or grow below this temperature (Lance 2003). The annual mean and coefficient of variation (cv) for precipitation included all months of the year. Temperature and precipitation values were assigned based on release year values and recapture year values as eight separate variables (e.g. release year mean temperature, recapture year mean temperature, etc.), however, the variable for hunter effort was only assigned based on recapture year. All values were assigned to individual alligator release-recapture records.

The following model served as the full GLMM model:

1.4
$$\begin{gathered}\log(\mathrm{n_{it}}) = \alpha + \beta_1(\text{time afield}) + \beta_2(\text{ release length}) + \\ \beta_3(\text{recapture length}) + \beta_4(\text{release length} * \text{time afield}) + \\ \beta_5(\text{recapture length} * \text{time afield}) + \beta_6(\text{ precipitation mean }) + \\ \beta_7(\text{precipitation cv}) + \beta_8(\text{temperature mean}) + \\ \beta_9(\text{temperature cv}) + \beta_9(\text{index of hunter effort}) + \\ \text{Etime afield, release length, recapture length,} \\ \text{precipitation mean, precipitation cv, temperature mean,} \\ \text{temperature cv, index of hunter effort} + \mathrm{z_{kt}}(\text{release year}) + \text{G release year.}\end{gathered}$$

Additional analyses included incorporating combinations of the covariates of interest into the models. Twenty-five biologically relevant hypotheses based on these combinations were decided upon and implemented as generalized linear mixed models (Table 3.2). Although not listed in the table, every attempted model also included the variables of release length, recapture length, and time afield. Additionally, each model also included the interaction terms between time afield and release and recapture lengths. Each of these models were assessed using the same fit statistics as above, separately for each sex.

All GLMM models were parameterized in SAS/STAT in PROC GLIMMIX (SAS Version 9.4, SAS Institute, Inc., Cary, NC). To derive survival estimates from the data, the LaPlace approximation (Wolfinger 1993, Schabenberger 2007, Gbur et al. 2012) in PROC GLIMMIX was selected as the best compromise between computation efficiency and reduced bias as compared with Guass-Hermite quadrature and penalized quasi-likelihood, respectively

(Bolker et al. 2008, Gbur et al. 2012). Survival estimates from each model are given in the form of instantaneous annual survival. In this context the GLMM models provide the predicted number of recaptures given the explanatory variables and covariates. This approach is analogous to the interpretation of survival from the slope of the exponential relationship between number recaptured with time (Ricker 1944). However, in the GLMM context rather than interpreting a single slope parameter, the entire model of explanatory variables and covariates are simultaneously interpreted as an estimate of survival. The advantage of this interpretation is the contribution of each explanatory variable or covariate can thus be partitioned into components of the GLMM. Converting instantaneous annual survival to annual survival can be achieved using exponentiation. The formula to estimate survival is:

1.5 $$z = e^{\alpha + B_1X_1 + \cdots + B_pX_p},$$

thus,

1.6 $$\hat{S}_i = z^{\text{year of interest}},$$

where z is the estimate of instantaneous annual survival and Si is the estimate of annual survival rate. The linear predictor for the model of interest is represented by $\alpha + B_1X_1 + \cdots + B_pX_p$ where α is the intercept, and B_pX_p refers to the combinations of covariates and their corresponding coefficients. Each X_p refers to the value of the mean for the explanatory variable it represents. By solving for the linear predictor and using exponentiation, instantaneous annual survival (z) can be estimated. To estimate survival for any other year, the value of instantaneous annual survival, z, is raised to the year of interest to provide an estimate of annual survival (S_i).

Because good fit was observed for several models, an ensemble of best fitting models were generated for both female and male alligators based on model averaging techniques (Bolker et al. 2008, Kéry and Royle 2016). Using the BIC (Bayesian or Schwartz's Information criterion) for each model and penalizing for the number of models evaluated, this technique generated a posterior probability for each model which indicates how much the data corresponding to each combination of variables supports the current model. Weighted coefficients were then generated based on the Bayesian model averaging technique for each variable in the best fitting models (Whitney and Ngo 2004, Grueber et al. 2011). Due to exceptionally close fit among the best fitting female models, five models with the highest posterior probabilities (>0.05) were selected for further model selection analysis. Vuong's (1989) non-nested hypothesis test was used to determine the best fitting model among the 5 female models with the highest probabilities (Lewis et al. 2010).

Table 3.2. Combination of covariates used in generalized linear mixed models (release length, recapture length, time afield, and interaction terms between time afield and release and recapture lengths were also included in each of the models).

Combinations of Covariates

Index of Hunter Effort	Mean Precipitation Temperature CV Index of Hunter Effort
Mean Precipitation Index of Hunter Effort	Mean Precipitation Precipitation CV
Mean Temperature	Mean Precipitation Precipitation CV Index of Hunter Effort
Mean Temperature Index of Hunter Effort	Mean Precipitation Precipitation CV Mean Temperature
Mean Temperature Temperature CV	Mean Precipitation Precipitation CV Mean Temperature Temperature CV Index of Hunter Effort

(Table 3.2 Continued)

Combinations of Covariates

Mean Temperature Temperature CV Index of Hunter Effort	Mean Precipitation Precipitation CV Mean Temperature Temperature CV
Temperature CV	Precipitation CV
Mean Precipitation	Precipitation CV Index of Hunter Effort
Mean Precipitation Mean Temperature	Precipitation CV Mean Temperature
Mean Precipitation Mean Temperature Index of Hunter Effort	Precipitation CV Temperature CV Index of Hunter Effort
Mean Precipitation Mean Temperature Temperature CV	Precipitation CV Temperature CV
Mean Precipitation Temperature CV	No Environment No Index of Hunter Effort

3.3 RESULTS:

Initial exploratory analyses built from the GLMM catch curve with a fixed intercept and negative binomial probability distribution was included as a proof of concept (Chapter 2), and once a baseline model for each sex was established, individual lengths were incorporated in the models along with environmental and hunter effort covariates from the year of recapture. Including these covariates from year of recapture improved model fit, with the best fitting models differing for female and male alligators (Tables 3.3 and 3.4). In addition to the combinations of the environmental and hunter effort covariates incorporated in the models, variables of release length, recapture length, time afield, and interaction terms between time afield and lengths were also included in all 25 of the models for each sex. Inclusion of climate data during the year of release did not improve fit among models for either sex, and are not included in further survival analyses.

Table 3.3 Attempted models, survival estimates, and corresponding fit for female alligators. $\hat{c}$ is $\frac{\chi^2}{df}$. RMSEA is the Root Mean Square Error of Approximation. Nagelkerke R^2 provides a measure of predictive power.

Model	Instantaneous Annual Estimate of Survival	$\hat{c}$	RMSEA	Nagelkerke R^2
Precipitation Mean	0.805	1.00	0.00	0.589
Precipitation Mean Precipitation CV	0.803	1.00	0.00	0.598
Precipitation Mean Temperature Mean	0.804	1.00	0.00	0.590
Temperature Mean Temperature CV Index of Hunter Effort	0.805	1.00	0.00	0.571
Precipitation Mean Temperature CV	0.805	1.01	0.006	0.549
Precipitation Mean Temperature Mean Index of Hunter Effort	0.805	1.01	0.006	0.590
Index of Hunter Effort	0.805	1.02	0.009	0.570
Temperature Mean Index of Hunter Effort	0.805	1.02	0.009	0.570
Precipitation Mean Index of Hunter Effort	0.805	1.03	0.012	0.591
Precipitation Mean Precipitation CV Temperature Mean Temperature CV	0.803	1.04	0.013	0.600
Precipitation Mean Temperature Mean Temperature CV	0.803	1.04	0.013	0.593
Precipitation CV Index of Hunter Effort	0.803	1.05	0.015	0.597
Precipitation Mean Temperature Mean Temperature CV Index of Hunter Effort	0.804	1.06	0.016	0.594
Precipitation mean Precipitation CV Temperature Mean Temperature CV Index of Hunter Effort	0.803	1.08	0.019	0.604

(Table 3.3 Continued)

Model	Instantaneous Annual Estimate of Survival	$\hat{c}$	RMSEA	Nagelkerke R^2
Precipitation Mean Temperature CV Index of Hunter Effort	0.803	1.12	0.024	0.585
Precipitation CV Temperature CV Index of Hunter Effort	0.801	1.13	0.025	0.593
Precipitation Mean Precipitation CV Index of Hunter Effort	0.802	1.15	0.026	0.601
Precipitation Mean Precipitation CV Temperature Mean	0.803	0.99	0.00	0.595
Precipitation CV	0.802	0.97	0.00	0.590
Precipitation CV Temperature CV	0.802	0.97	0.00	0.590
Precipitation CV Temperature Mean	0.802	0.97	0.00	0.590
No environment or Hunter Effort Covariates	0.805	0.96	0.00	0.565
Temperature Mean	0.804	0.96	0.00	0.565
Temperature CV	0.804	0.95	0.00	0.566
Temperature Mean Temperature CV	0.805	0.95	0.00	0.566

Table 3.4. Attempted models, survival estimates, and corresponding fit for male alligators. $\hat{c}$ is $\frac{\chi^2}{df}$. RMSEA is the Root Mean Square Error of Approximation. Nagelkerke R^2 provides a measure of predictive power.

Model	Instantaneous Annual Estimate of Survival	$\hat{c}$	RMSEA	Nagelkerke R^2
Precipitation Mean Precipitation CV Index of Hunter Effort	0.785	1.08	0.02	0.488
Precipitation CV Temperature CV Index of Hunter Effort	0.784	1.08	0.02	0.482
Precipitation Mean Temperature CV Index of Hunter Effort	0.785	1.15	0.027	0.516
Precipitation Mean Temperature CV	0.790	0.98	0.00	0.526

(Table 3.4 Continued)

Model	Instantaneous Annual Estimate of Survival	$\hat{c}$	RMSEA	Nagelkerke R^2
Precipitation Mean Precipitation CV Temperature Mean Temperature CV Index of Hunter Effort	0.791	0.97	0.00	0.528
Precipitation Mean Temperature Mean Temperature CV Index of Hunter Effort	0.790	0.97	0.00	0.528
Precipitation Mean Precipitation CV Temperature Mean Temperature CV	0.791	0.97	0.00	0.526
Precipitation Mean Temperature Mean Temperature CV	0.791	0.97	0.00	0.526
Precipitation Mean	0.790	0.94	0.00	0.494
Precipitation Mean Index of Hunter Effort	0.790	0.94	0.00	0.495
Precipitation Mean Precipitation CV	0.790	0.94	0.00	0.494
Precipitation Mean Temperature Mean	0.792	0.93	0.00	0.510
Precipitation Mean Temperature Mean Index of Hunter Effort	0.792	0.92	0.00	0.511
Precipitation Mean Precipitation CV Temperature Mean	0.797	0.92	0.00	0.509
Precipitation CV Temperature CV	0.792	0.92	0.00	0.488
Precipitation CV Index of Hunter Effort	0.790	0.91	0.00	0.482
Index of Hunter Effort	0.790	0.91	0.00	0.479
Precipitation CV Temperature Mean	0.790	0.91	0.00	0.480
Precipitation CV	0.791	0.91	0.00	0.480
Temperature CV	0.790	0.91	0.00	0.483
Temperature Mean Index of Hunter Effort	0.791	0.90	0.00	0.495
Temperature Mean Temperature CV Index of Hunter Effort	0.791	0.90	0.00	0.495

(Table 3.4 Continued)

Model	Instantaneous Annual Estimate of Survival	$\hat{c}$	RMSEA	Nagelkerke R^2
No Environment or Market Covariates	0.791	0.90	0.00	0.477
Temperature Mean Temperature CV	0.791	0.90	0.00	0.491
Temperature Mean	0.791	0.89	0.00	0.490

As described in the Methods, a model was determined to have good fit if the $\hat{c}$ value was between 1 and 2 (Gbur et al. 2012) and the RMSEA value was below 0.05 (Browne et al. 1993). For Nagelkerke (1991) R^2, higher values are preferred as this value indicates stronger predictive power of the model (Tjur 2009).

Of the 25 biologically relevant models generated for these analyses for each sex, 17 models provided good fit for females (Table 3.5), and 3 provided good fit for males (Table 3.6). Due to having more than one model with good fit, Bayesian posterior probabilities were generated as an additional measure for interpretation, to determine how much the data corresponding to each combination of variables contributed to model fit (Tables 3.5 and 3.6). Weighted coefficients based on the posterior probabilities were computed for each variable in each model (Whitney and Ngo 2004).

Table 3.5. Covariates from best fitting female models, the posterior probability of the model, and weighted coefficient for each included variable.

Model	Posterior Probability of Model	Weighted Coefficient for Each Variable in Model
Intercept	0.290	-1.739
Time Afield		0.374
Release Length		0.009
Recapture Length		0.032
Time Afield * Release Length		-0.002
Time Afield * Recapture Length		-0.004
Precipitation Mean		-0.030
Precipitation CV		0.002
Intercept	0.246	-1.823
Time Afield		0.339
Release Length		0.008
Recapture Length		0.028
Time Afield * Release Length		-0.001
Time Afield * Recapture Length		-0.004
Precipitation CV		0.003
Index of Hunter Effort		0.002
Intercept	0.137	-0.658
Time Afield		0.170
Release Length		0.004
Recapture Length		0.014
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		-0.002
Precipitation Mean		-0.021
Intercept	0.127	-1.035
Time Afield		0.200
Release Length		0.006
Recapture Length		0.015
Time Afield * Release Length		-0.001
Time Afield * Recapture Length		-0.002
Precipitation Mean		-0.009
Precipitation CV		0.001
Index of Hunter Effort		0.001
Intercept	0.047	-0.247
Time Afield		0.061
Release Length		0.001
Recapture Length		0.005
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		-0.007
Index of Hunter Effort		<0.001

(Table 3.5 Continued)

Model	Posterior Probability of Model	Weighted Coefficient for Each Variable in Model
Intercept	0.032	-0.112
Time Afield		0.041
Release Length		0.001
Recapture Length		0.003
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		-0.005
Temperature Mean		<0.001
Intercept	0.023	-0.026
Time Afield		0.029
Release Length		<0.001
Recapture Length		0.002
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Precipitation mean		-0.003
Precipitation CV		<0.001
Temperature Mean		-0.001
Temperature CV		-0.001
Intercept	0.016	-0.170
Time Afield		0.027
Release Length		0.001
Recapture Length		0.002
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Precipitation CV		<0.001
Temperature CV		<0.001
Index of Hunter Effort		<0.001
Intercept	0.015	0.003
Time Afield		0.018
Release Length		<0.001
Recapture Length		0.001
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		-0.002
Temperature Mean		<0.001
Temperature CV		-0.001

(Table 3.5 Continued)

Model	Posterior Probability of Model	Weighted Coefficient for Each Variable in Model
Intercept		-0.005
Time Afield		0.005
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	0.004	<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		<0.001
Temperature Mean		<0.001
Temperature CV		<0.001
Index of Hunter Effort		<0.001
Intercept		-0.014
Time Afield		0.003
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	0.002	<0.001
Time Afield * Recapture Length		<0.001
Temperature Mean		<0.001
Index of Hunter Effort		<0.001
Intercept		-0.016
Time Afield		0.003
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	0.001	<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		<0.001
Temperature CV		<0.001
Index of Hunter Effort		<0.001
Intercept		-0.007
Time Afield		0.001
Release Length		<0.001
Recapture Length	0.001	<0.001
Time Afield * Release Length		<0.001
Time Afield * Recapture Length		<0.001
Index of Hunter Effort		<0.001

(Table 3.5 Continued)

Model	Posterior Probability of Model	Weighted Coefficient for Each Variable in Model
Intercept		<0.001
Time Afield		<0.001
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	<0.001	<0.001
Time Afield * Recapture Length		<0.001
Temperature Mean		<0.001
Temperature CV		<0.001
Index of Hunter Effort		<0.001

Table 3.6. Covariates from best fitting male models, the posterior probability of the model, and weighted coefficient for each included variable.

Model	Posterior Probability of Model	Weighted Coefficient for Each Variable in Model
Intercept		-1.421
Time Afield		0.689
Release Length		0.023
Recapture Length		0.082
Time Afield * Release Length	0.994	-0.006
Time Afield * Recapture Length		-0.008
Temperature CV		-0.152
Precipitation Mean		-0.202
Index of Hunter Effort		0.006
Intercept		-0.004
Time Afield		<0.001
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	0.001	<0.001
Time Afield * Recapture Length		<0.001
Temperature CV		<0.001
Precipitation CV		<0.001
Index of Hunter Effort		<0.001
Intercept		-0.014
Time Afield		0.002
Release Length		<0.001
Recapture Length		<0.001
Time Afield * Release Length	0.004	<0.001
Time Afield * Recapture Length		<0.001
Precipitation Mean		<0.001
Precipitation CV		<0.001
Index of Hunter Effort		<0.001

Of the 3 best fitting male models, there was overwhelming support based on the posterior probabilities (0.99), for the model containing the covariate combination of mean precipitation, temperature cv, and index of hunter effort. Based on $\hat{c}$, RMSEA, Nagelkerke R^2 (1991), and Bayesian posterior probabilities, the best fitting male model was:

1.7
$$\begin{gathered}\log(\mathrm{n_{it}}) = (-1.428 + 0.689(\text{time afield}) + \\ 0.023(\text{ release length}) + 0.082(\text{recapture length}) - \\ 0.006(\text{release length} * \text{time afield}) - 0.008(\text{recapture length} * \\ \text{time afield}) - 0.153(\text{ temperature cv}) - \\ 0.203(\text{precipitation mean}) + 0.006(\text{ index of hunter effort}) + \\ \mathrm{E}\ (\text{timeafield, release length, recapture length, tempearature cv, precipitation mean,} \\ \text{index of hunter effort}) + \mathrm{z_{kt}}(\text{release year}) + \mathrm{G}(\text{release year}).\end{gathered}$$

The parameter $\mathrm{z_{kt}}$ was unique for each release year and not shown to save space. The best fitting male model had a RMSEA value of 0.027 and a $\hat{c}$ value of 1.15. The fit statistics for the best fitting male model indicate good fit and minimal overdispersion within the data using the negative binomial probability distribution. Temperature cv and precipitation mean were both statistically significant in the male model with ($F_{1,169}$=7.19, p<0.05) and ($F_{1,169}$=12.51, p<0.05), respectively. The interaction term between time afield and length at release in this model was also statistically significant for male alligators ($F_{1,169}$=5.62, p<0.05). Although the inclusion of the covariate associated with index of hunter effort improved model fit, it was not found to be statistically significant.

Of the 17 models with good fits for females, there was no single model with an overwhelmingly high Bayesian posterior probability, and a cutoff based on the top 5 highest probabilities was used. Vuong's (1989) non-nested hypothesis test was then used to determine which of the top 5 female models provided the best fit (Lewis et al. 2010).

Based on $\hat{c}$ values, RMSEA values, Nagelkerke's R^2, Bayesian posterior probabilities, and Vuongs (1989) non-nested hypothesis test, the best fitting female model was:

1.8
$$\log(n_{it}) = (-4.803 + 1.240(\text{time afield}) + 0.029(\text{ release length}) + 0.108(\text{recapture length}) - 0.007(\text{release length} * \text{time afield}) - 0.016(\text{recapture length} * \text{time afield}) - 0.158(\text{ precipitation mean }) + E(\text{timeafield}, \text{release length}, \text{recapture length}, \text{precipitation mean}) + z_{kt}(\text{release year}) + G(\text{release year}).$$

The parameter z_{kt} was unique for each release year and not shown to save space. The best fitting female model had a RMSEA value of 0.00 and a $\hat{c}$ value of 1.00 indicating good fit and provided confirmation that overdispersion within the data when using the negative binomial distribution is not a factor. Mean precipitation during the year of recapture was statistically significant in this model ($F_{1,180}$=12.33, $p<0.05$) along with the interaction term between time afield and length at release for female alligators ($F_{1,180}$=5.89, $p<0.05$).

The best fitting models estimated instantaneous annual survival to be 0.785 and 0.805, for male and female alligators, respectively. Annual survival estimates can be computed for any year from the estimates of instantaneous annual survival provided by the best fitting models (Formulas 1.5 and 1.6) (Ricker 1944). Using formula 1.5 to estimate instantaneous annual survival (z), formula 1.6 can then be used to determine overall survival (S_i). For example, if survival during year 9 was of interest for female alligators, one would raise 0.805 to the ninth degree, $S_i = 0.805^9$, to get a value of 0.141. This means that overall annual survival after a female alligator has been afield for nine years is estimated to be 0.141, given the data available to date. Annual estimates of survival were estimated for female and male alligators throughout the time span of the current data set (Tables 3.7 and 3.8).

Table 3.7. Estimates of annual survival and confidence intervals for female alligators.

Years Since Release	Survival	Lower 95%	Upper 95%
1	0.805	0.783	0.827
2	0.648	0.613	0.683
3	0.521	0.480	0.565
4	0.419	0.375	0.467
5	0.338	0.294	0.386
6	0.272	0.230	0.319
7	0.219	0.180	0.264
8	0.176	0.141	0.218
9	0.141	0.110	0.180
10	0.114	0.086	0.149
11	0.091	0.067	0.123
12	0.074	0.053	0.102
13	0.059	0.041	0.084
14	0.047	0.032	0.069
15	0.038	0.025	0.057
16	0.031	0.019	0.047
17	0.025	0.015	0.039
18	0.020	0.012	0.032
19	0.016	0.009	0.027
20	0.013	0.007	0.022
21	0.010	0.005	0.018
22	0.008	0.004	0.015
23	0.006	0.003	0.012

Table 3.8. Estimates of annual survival and confidence intervals for male alligators.

Years Since Release	Survival	Lower 95%	Upper 95%
1	0.785	0.761	0.809
2	0.616	0.579	0.654
3	0.483	0.440	0.529
4	0.379	0.335	0.428
5	0.298	0.255	0.346
6	0.234	0.194	0.280
7	0.183	0.147	0.226
8	0.144	0.112	0.183
9	0.113	0.085	0.148
10	0.088	0.065	0.120
11	0.069	0.049	0.097
12	0.054	0.037	0.078
13	0.042	0.028	0.063
14	0.033	0.021	0.051

(Table 3.8 Continued)

Years Since Release	Survival	Lower 95%	Upper 95%
16	0.020	0.012	0.033
17	0.016	0.009	0.027
18	0.012	0.007	0.022
19	0.010	0.005	0.017
20	0.007	0.004	0.014
21	0.006	0.003	0.011
22	0.004	0.002	0.009
23	0.003	0.001	0.007

The log of the number of alligators recaptured plotted against time afield and release length, for both male and female alligators respectively, is presented to show the slopes from where survival estimates for instantaneous annual survival are computed using the formula from Ricker (1944) in the best fitting models (Figures 3.1 and 3.2).

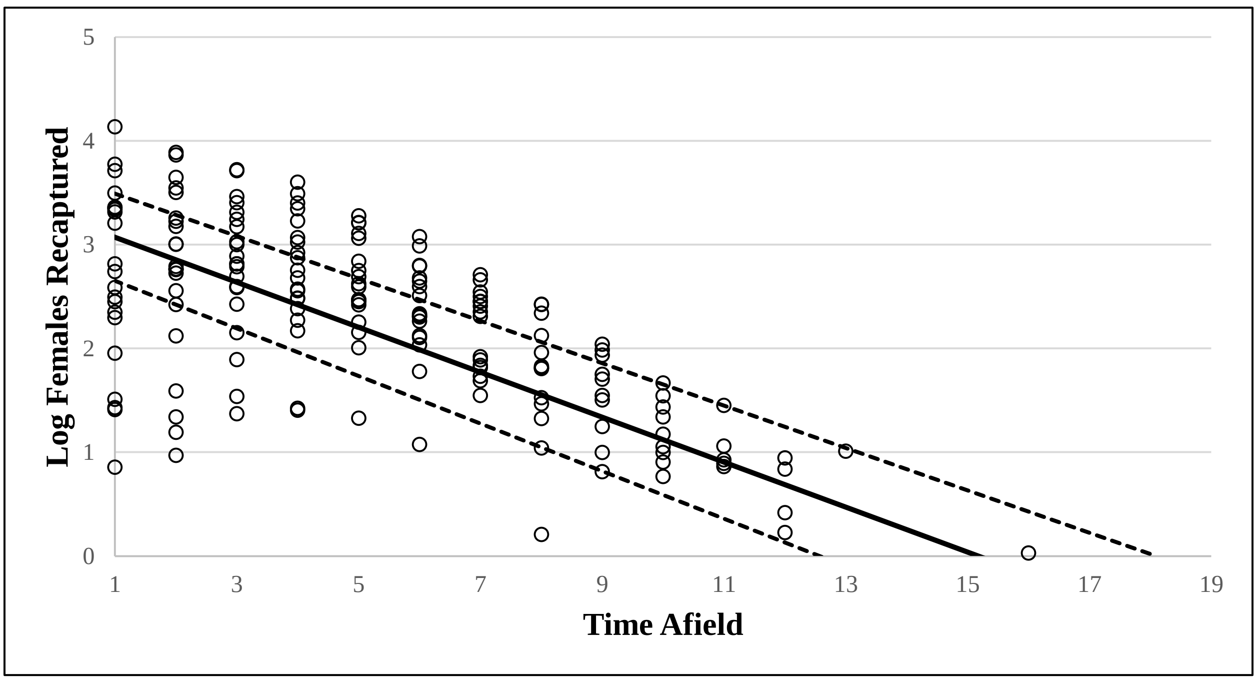

Figure 3.1. Relationship between observed log number of females recaptured and time afield. Circles represent observed log of recaptured females, whereas the solid line is the model estimated log number of recaptures. Dotted lines represent 95% confidence intervals.

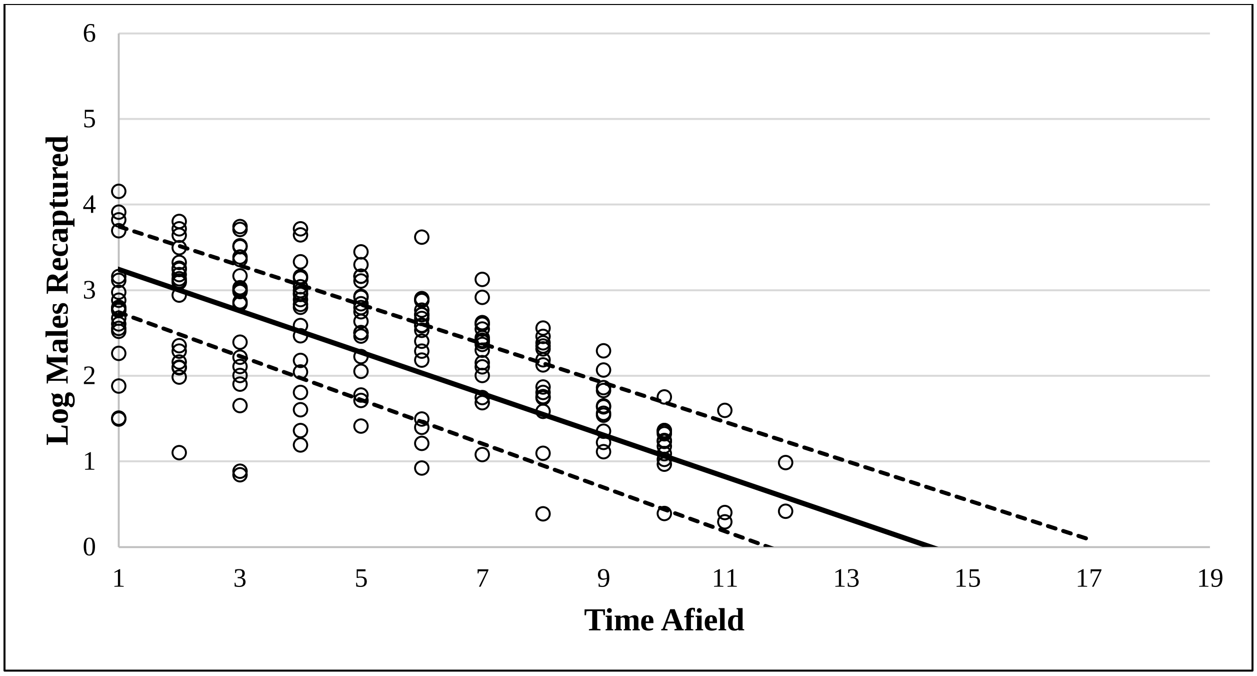

Figure 3.2. Relationship between observed log number of males recaptured and time afield. Circles represent observed log of recaptured males, whereas the solid line is the model estimated log number of recaptures. Dotted lines represent 95% confidence intervals.

Plots from the back transformed data are also presented to provide clarification (Figures 3.3 and 3.4). The graphs from Chapter 2 for the best fitting GLMM are also provided (Figures 3.5 and 3.6) to show the differences in the model once environmental and hunter effort covariates were included. The confidence intervals for the graphs representing the GLMM without covariates (Figures 3.5 and 3.6) are narrower. The wider confidence intervals for the model including covariates (Figures 3.3 and 3.4) is explained by the extra variation in estimates associated with the edition of these variables. However, beginning around years 5 to 7, the confidence intervals appear to be more similar, suggesting that the added covariates influence survival more during the 5 to 7 years following release.

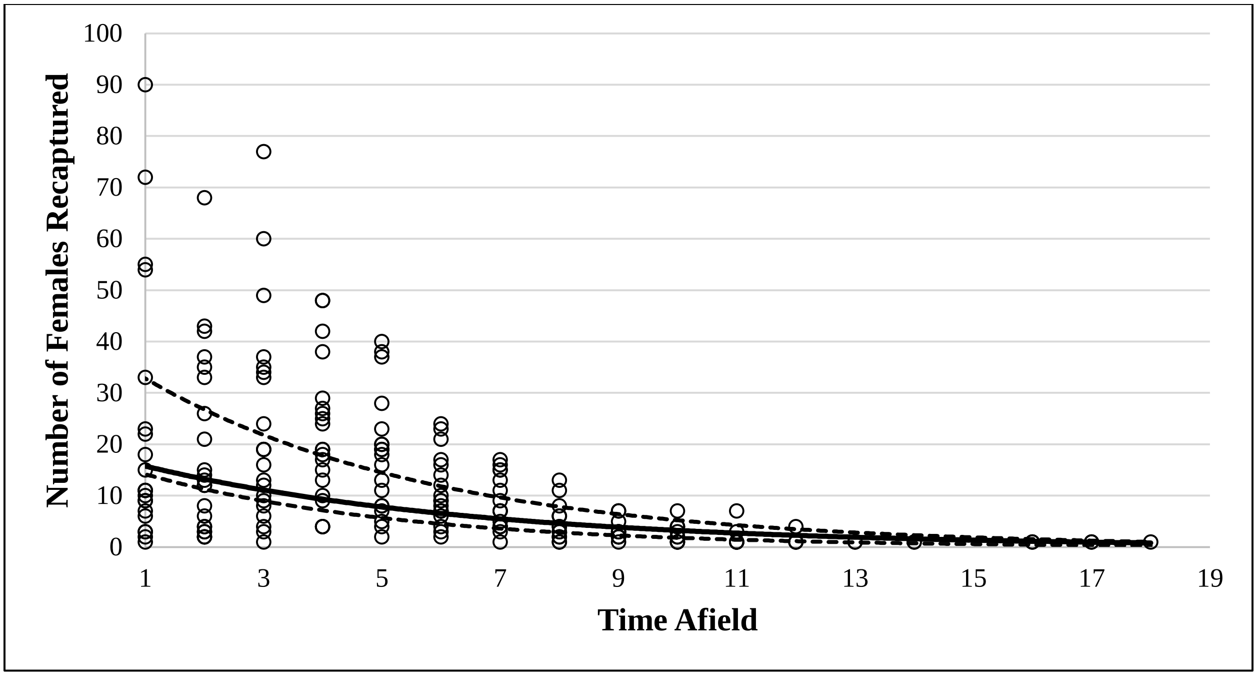

Figure 3.3. Relationship between observed number of females recaptured and time afield with the inclusion of environmental covariates. Circles represent observed recaptured females, whereas the solid line is the model estimated number of recaptures. Dotted lines represent 95% confidence intervals.

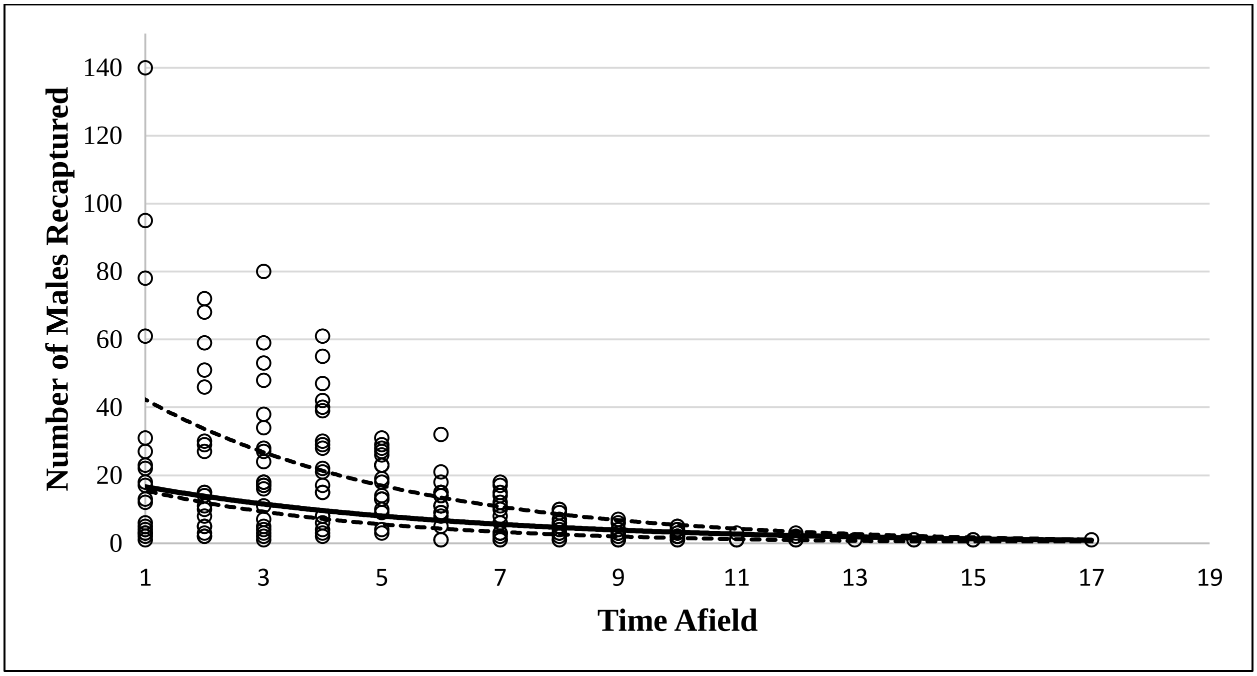

Figure 3.4. Relationship between observed number of males recaptured and time afield with the inclusion of environmental and hunter index covariates. Circles represent observed recaptured males, whereas the solid line is the model estimated number of recaptures. Dotted lines represent 95% confidence intervals.

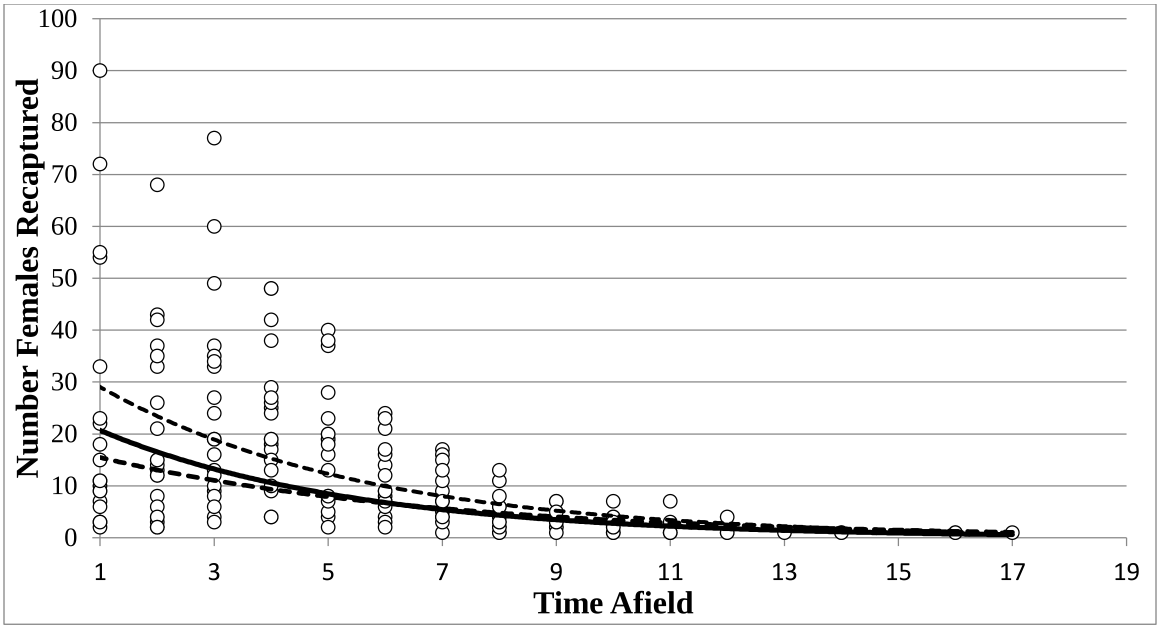

Figure 3.5. Relationship between observed number of females recaptured and time afield without environmental covariates added. Circles represent observed recaptured females, whereas the solid line is model estimated the number of recaptures. Dotted lines represent 95% confidence intervals.

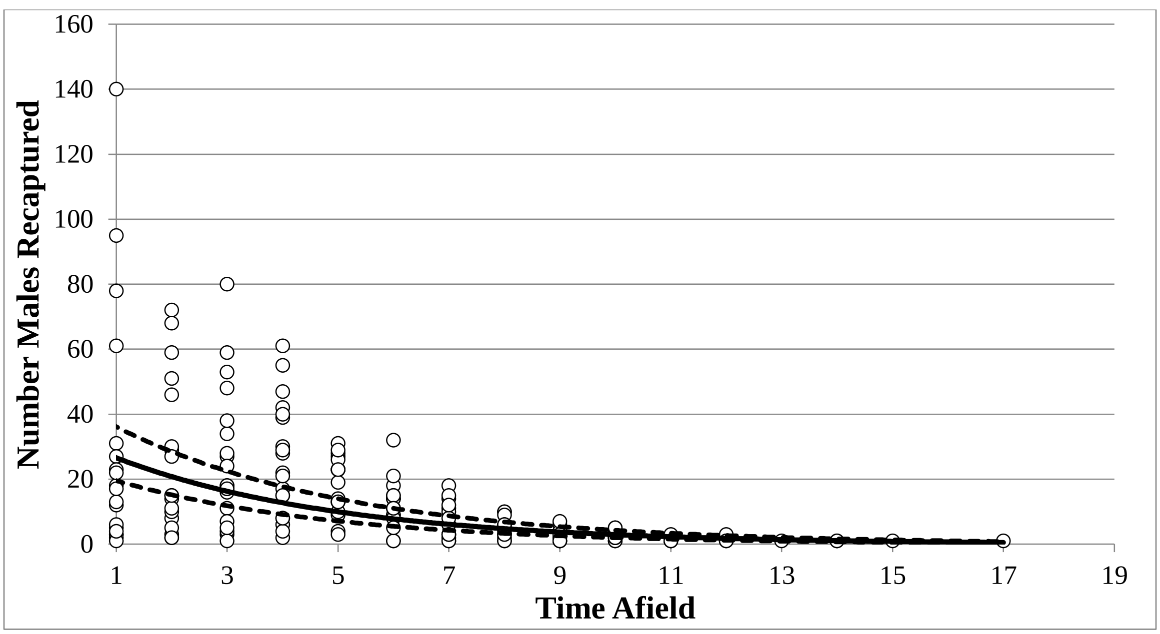

Figure 3.6. Relationship between observed number of males recaptured and time afield without environmental or hunter index covariates added. Circles represent observed recaptured males, whereas the solid line is the model estimated number of recaptures. Dotted lines represent 95% confidence intervals.

ARIMA models detected significant temporal correlation (> 2 standard errors autocorrelation function) between the number of recaptured alligators with hunter effort for the current year through two years prior to harvest. However, none of the hunter effort models from ARIMA improved fit.

ARIMA cross-correlation analyses indicated significant temporal correlation (> 2 standard errors autocorrelation function) between the number of recaptured alligators with mean temperature during the time periods 7-13 and 15-20 years prior to harvest. However, when included in survival models these time periods did not improve model fit and the temperature variables were not statistically significant. ARIMA models did not detect any temporal correlations with precipitation.

3.4 DISCUSSION:

The best fitting models suggested that environmental and hunter effort covariates, during the year of recapture, modify the influence of release length on the survival of ranch-released alligators following the initial release period, dependent upon sex. Previous modeling efforts to establish a baseline model without release length, or the environmental and hunter effort covariates, estimated female instantaneous annual survival to be 0.890, and male instantaneous annual survival to be 0.870 (Chapter 2).

Environment and Index of Hunter Effort:

The difference (0.085) in the estimated female survival between the baseline (0.890) and model with environmental conditions (0.805) may be interpreted as the influence of varying environmental conditions on survival. Among female alligators, wetter years increased survival, and the difference between a best conditions estimate (0.890) compared with environmental conditions adjusted estimate (0.805) illustrates the reduced survival associated with drier years. Release length is an important influence on survival for female alligators, indicating that the larger a female alligator is at release, the better chance of survival (i.e. alligator is not harvested), and the longer it will be afield.

The difference (0.085) in the estimated male survival between the baseline (0.870) and model with environmental and hunter effort covariates (0.785), may be interpreted the same way as females, in that environmental conditions (and hunter effort for males) influence survival. As with females, wetter years increase survival for males, and the difference (0.085) between the baseline and the conditions adjusted estimate illustrates reduced survival with drier years. In addition to precipitation, variations in temperature between months, as indicated by the covariate temperature cv, was also statistically significant. Survival was negatively associated with temperature cv suggesting reduced survival among years that are more variable in temperature between months. Release length is also an important influence on survival for male alligators, indicating that the larger a male alligator is at release the better chance of survival (i.e. alligator is not harvested), and the longer it will be afield.

In addition to the statistically significant variables and environmental covariates, the best fitting male model also included the index of hunter effort. Although index of hunter effort was not statistically significant in the best fitting male model, overall fit was reduced with the removal of this covariate. The difference in fit with the removal of the index of hunter effort, suggested that the inclusion of this covariate contributes information important for the analysis of the survival for male alligators, although not sufficient to cross thresholds of statistical significance. This is most likely related to the influence of market prices on the behavior of hunters. If prices are high, hunters may be more selective toward targeting larger alligators resulting in fewer recaptures of tagged alligators, with the opposite scenario occurring if prices are low (Elsey et al. 1998).

Because alligators have been in existence as a species for many years (Green et al. 2014) and have been observed using avoidance strategies that allow them to survive periods of environmental stress such as droughts and variations in temperature (McIlhenny 1935, Chabreck 1965, Hayes-Odum and Jones 1993), it is unlikely that the link between climatic variables with survival is direct. Documented cases of alligators suffering direct morality from hurricanes (Lance et al. 2010), cold shock (Brisbin et al. 1982, Lance and Elsey 1999), and salt water intrusion from hurricanes (Ensminger and Nichols 1957) have been reported. However, in these same studies, alligators appeared to be resilient, and the population as a whole was not severely affected as a result of these factors (Ensminger and Nichols 1957, Lance and Elsey 1999, Lance et al. 2010). It is more likely that the influence of dry years for male and female alligators in this study in southwest Louisiana, and variable temperature for males, are indirectly affecting the survival of these alligators due to difference in behavior (Mazzotti et al. 2009) responding to reduced habitat, reduced forage, or lack of heterogeneity in hydrology (Brandt et al. 2016). Habitat type, water depth, and prey availability (CPRA 2012, Nyman et al. 2013) may play a role in the survival to harvest of the alligators included in this dataset, but data regarding these factors were not accessible and therefore were not included with these analyses.

Only months with mean temperatures sufficient for alligator activity (>16˚ C) were included in the models due to the physiology of alligators (Lance 2003). Precipitation means were not modified in this way because of the importance of this variable on the location of alligators, even when they are not feeding or growing. Years with higher water levels provide more habitat for alligators, allowing them to travel into areas that may not be accessible during low rain years (Chabreck 1965, Joanen and McNease 1972). In addition to accessibility, higher water levels keep salinities at a tolerable level as increased salinities have been observed to result in the movement of alligators in search of fresh water (Chabreck 1965, Hayes-Odum and Jones 1993, Mazzotti et al. 2009) and lower body mass conditions in juveniles (Deitz 1979, Mazzotti et al. 2009). This increase in habitat availability potentially reduces cannibalism, and other harmful density related events such as disease and lower food availability (Deitz 1979, Woodward et al. 1987, Hayes-Odum and Jones 1993, Mazzotti et al. 2009).

Because alligator behavior is closely linked to thermoregulation (Chabreck 1965, Joanen and McNeese 1972, Smith 1979, Lang 1987), variations in temperature could result in differing behaviors and may be one explanation as to why the coefficient of variation for male alligators was statistically significant in the best fitting model. Dependent on the size of an alligator, different physiological and behavioral thermoregulation occurs (Terpin et al. 1979, Seebacher et al 2003). Variations in air and water temperature play a role in the location of an alligator at any given time. For example, when air temperature is warmer than water temperature, basking behaviors are observed within and outside of the water. Alligators may retreat to deeper water if the opposite is experienced. Microhabitat selection is important for small and medium alligators, as it is harder for them to thermoregulate via physiological process therefore, location is particularly important (Smith 1979). In a telemetric study conducted by Joanen and McNeese (1972) on male alligators in southwest Louisiana, distances traveled and habitat choice were attributed to temperature. A preference for canals was observed, possibly because of the buffering effect experienced by this deeper water during temperature extremes of both summer and winter seasons (Joanen and McNeese 1972, Seebacher et al 2003). It was also noticed during this study that activity of alligators varied seasonally. During the summer more activity occurred at night, whereas during the cooler months, more activity was observed during the day (Joanen and McNeese 1972). The correlation of temperature and behavior may provide insight into the lower survival experienced by male alligators during years with more variation in temperature between months as changing temperatures can be stressors (Lance and Elsey 1999). Because the movement of alligators is correlated with temperature, an alligator will need to move more if the temperature is more variable in order to maintain a suitable internal temperature. During these movements alligators may move into the territory of another alligator resulting in fighting (Garrick and Lang 1977, Lang 1987) or cannibalism (Rootes and Chabreck 1993). Additionally, this increased movement may result in a higher probability of coming in contact with a vehicle or hunter, resulting in mortality.

The stage-based population model used by Dunham et al. (2014), focused on varying climate scenarios to determine the effects on the population viability of northern populations of alligators. Although literature values were used for their analyses, the models constructed showed that northern populations would be negatively impacted by the combined effects of the projected increase in temperature and decrease in precipitation (Dunham et al. 2014). Whereas the results were focused on northern populations, the same impacts can be speculated for southern populations as the physiology of the species is the same. Lower habitat availability as a result of less precipitation in combination with higher temperatures could also negatively impact the habitat of alligators in Louisiana potentially resulting in lower survival (Hayes-Odum and Jones 1993, Nyman et al. 2013).

Release Length:

In the best fitting models for both male and female alligators, the interaction term between release length and time afield was statistically significant. Due to the release length variable being significant and positively associated with survival in the best fitting models, additional analyses were conducted for each sex to further examine the effect of release length. Data were plotted, and 3 length categories were used due to natural breaks observed within the data (Figures 3.7 and 3.8).

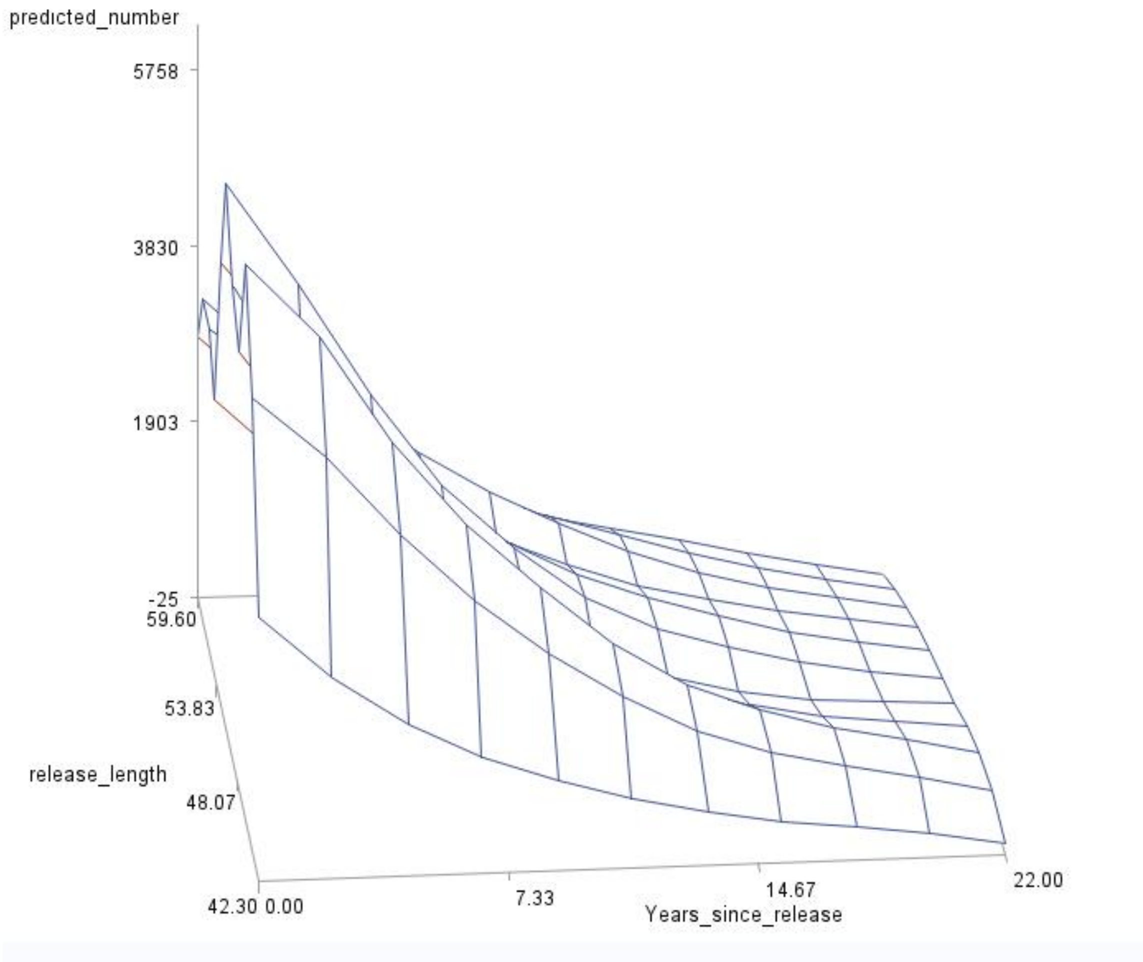

Figure 3.7. Smoothed predicted number of recaptured female alligators given release length and years since release (time afield).

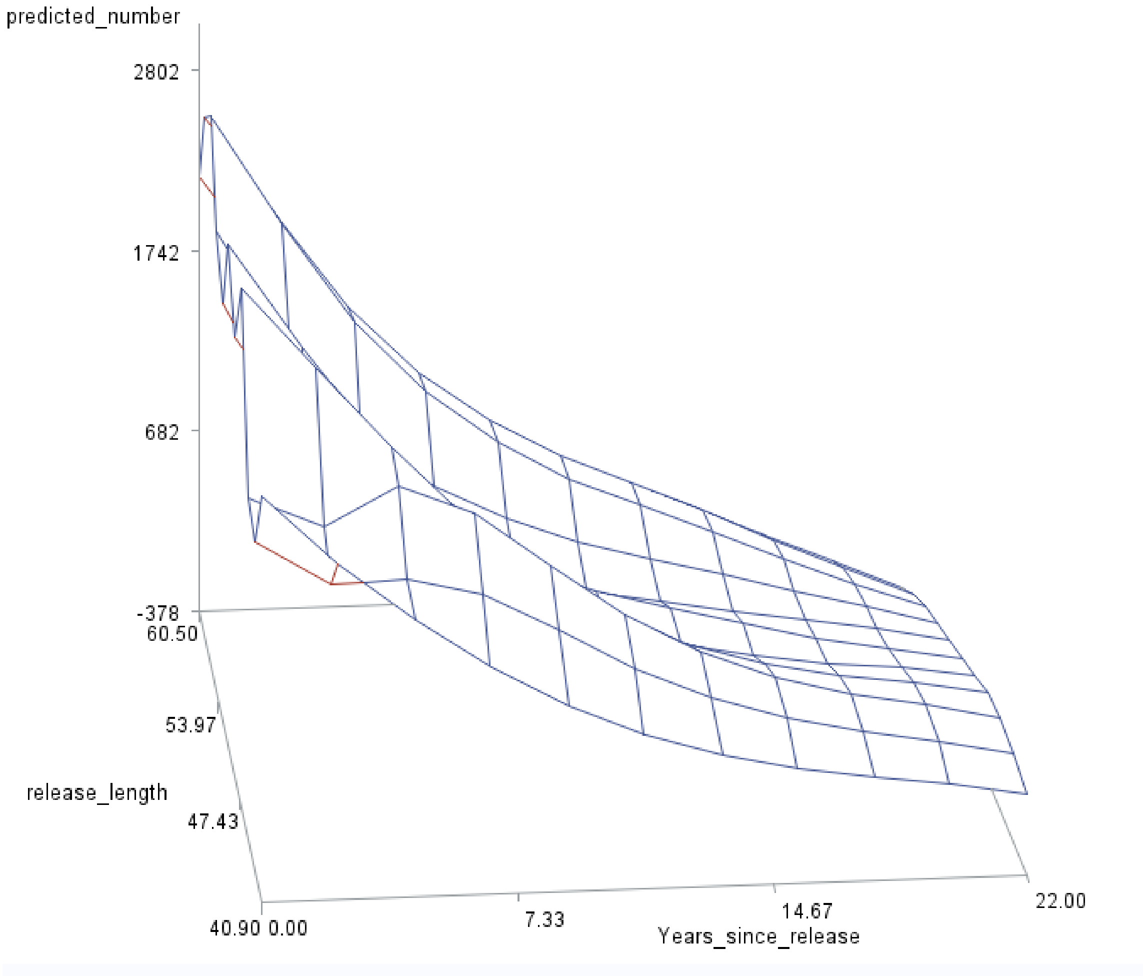

Figure 3.8. Smoothed predicted number of recaptured male alligators given release length and years since release (time afield).

Alligators with lengths at release greater than 139 cm (55 inches) were considered ‘large’, alligators with lengths between 101 cm (40 in) and 139 cm (55 in) were considered ‘medium’, and alligators with lengths less than 101 cm (40 in) were considered ‘small’.

Using the grouping categories based on release length, it was found that increasing release length had a positive influence on increasing survival to a certain point (benefits diminish after 139 cm) (Tables 3.9 and 3.10).

Table 3.9. Estimates of female instantaneous annual survival based upon size at release.

Size at Release	Estimate of Instantaneous Annual Survival
Small < 101 cm	NA
Medium 101 -139 cm	0.892
Large >139 cm	0.823

Table 3.10. Estimates of male instantaneous annual survival based upon size at release.

Size at Release	Estimate of Instantaneous Annual Survival
Small < 101 cm	NA
Medium 101 -139 cm	0.882
Large >139 cm	0.831

Instantaneous annual survival rates for female alligators were estimated to be 0.823 for the large group, and 0.892 for the medium group. Survival rates could not be reliably estimated for the small group because of a small sample size suggesting that alligators that are small when released are subject to high mortality as they contribute little to the annual harvest, which was also suggested by Elsey et al. (1998). Within the large and medium female groups, survival was higher than the overall estimated instantaneous survival rate of 0.805. These results suggest that releasing alligators greater than 101 cm (40 in) improves their survival to harvest rates. However, the higher survival rate within the medium group compared to the large group suggests that the large alligators attain a harvestable size much quicker, resulting in higher harvest rates than medium alligators (Figure 3.9).

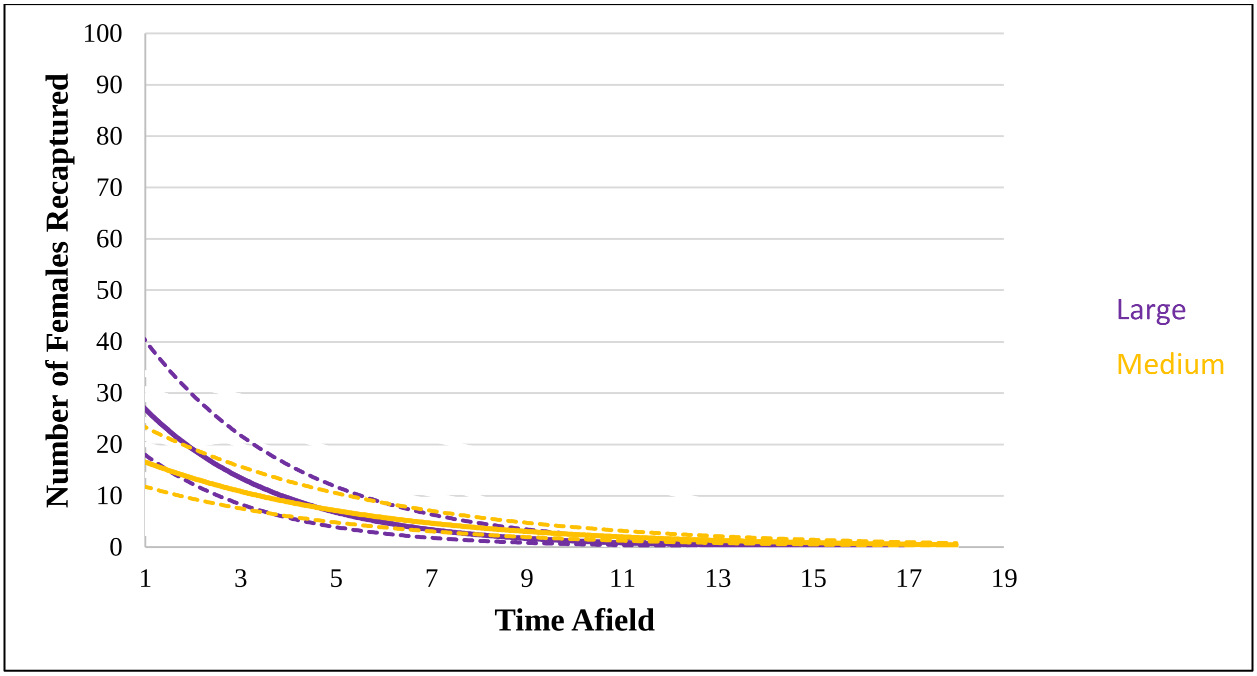

Figure 3.9. Plot of expected recaptures of medium (101-139 cm; gold), and large (>139 cm; purple) female alligators over time.

The same trend for females is also seen for males. Estimated instantaneous survival rates for male alligators were 0.831 and 0.882, for the large and medium groups, respectively. The small sample size for small male alligators resulted in unreliable parameter estimates suggesting lowered survival for released alligators of this size. As for females, the medium and large male alligators have higher survival rates compared to the overall survival rate of 0.785, and larger alligators have higher harvest rates than medium alligators.

This again suggests that male alligators that are large (>139 cm) when released attain a harvestable size more quickly (Figure 3.10).

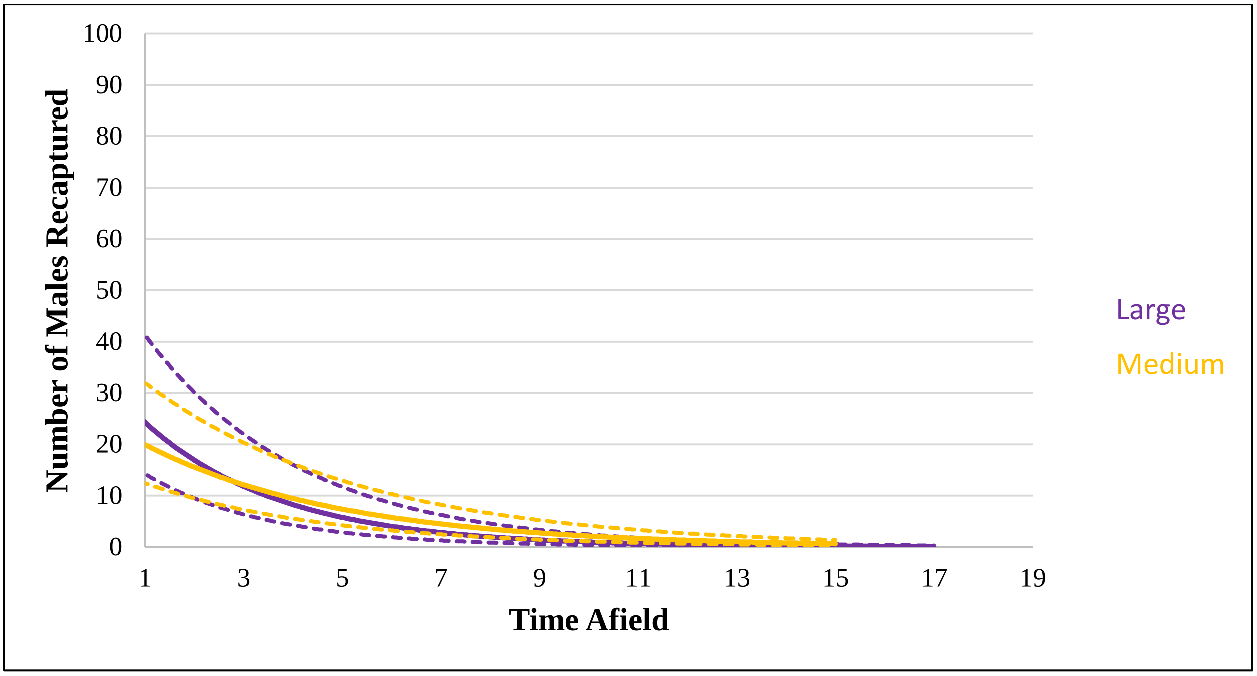

Figure 3.10. Plot of expected recaptures of medium (101.6-139 cm; gold), and large (>139 cm; purple) male alligators over time.

If the line of best fit for recaptured alligators for medium and large individuals is examined, it can be seen that after year 4 for females, and year 3 for males, the survival of these groups appears to be similar. This suggests that after 3 to 4 years of being afield, size at release is no longer a factor, and the rate of survival to harvest for these two size groups are the same.

3.5 SUMMARY:

In conclusion, analyses on primary data suggested that temperature and precipitation affected survival to harvest rates, supporting the conclusions of the literature based wild alligator model of Dunham et al. (2014). Moreover, this modeling effort added new findings on the role of length on alligator survival. Finally, akin to the similar survival patterns observed between wild

(Nichols et al. 1976, Taylor and Neal 1984) and ranch-released alligators (this study), the similarity in response to temperature and precipitation between this study and the findings of Dunham et al. (2014) suggest that the conclusions of this study may have some level of applicability to wild populations of alligators in Louisiana as well. Based on these results, further research into the role of environmental variables upon survival wild alligators is warranted.

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CHAPTER 4: CONCLUSION

4.1 DISCUSSION:

Although there are a number of models for the purpose of survival analyses, the results from the analyses of the alligator data clearly selected the generalized linear mixed model (GLMM) catch curve with a fixed intercept and negative binomial distribution as the best fitting model. The unique ecology of the American alligator and the management of this species in Louisiana resulted in the failure of many of the traditional models typically used for this type of analyses. Our results demonstrated that the survival to harvest following the first period of release of American alligators in southwest Louisiana was related to release length, and modified by environmental factors and/or hunter effort, depending on sex. By accounting for natural variability, the estimates for the influence of release length on survival became more accurate and precise. Although the effects differed by sex, both male and female survival were influenced by mean precipitation during the year of recapture, with decreased survival during drier years. Male alligator survival was additionally dependent and negatively associated with the coefficient of variation for temperature during months that were above 16˚ C, indicating that wide variability in mean temperatures decreased survival. The survival of both sexes was additionally influenced by release length, with results suggesting that the larger alligators are upon release the better their survival, and the longer they will be afield prior to possibly being harvested. Further analysis of the release length variable indicated that alligators in the 101 to 139 cm (40 to 55 in) range when released had the highest rate of survival, with this rate seemingly diminishing for alligators above 139 cm (55 in) as they appear to not survive as long, because they reach a harvestable size sooner. Alligators less than 101 cm (40 in) when released contributed very little to the annual harvest and presumably experience high mortality.

It is important to note that this analysis is retrospective requiring the knowledge of the complete precipitation and temperature patterns of recapture years, and although the understanding of the release length-survival relationship is enhanced, the management implications of release length upon survival to harvest have not changed by inclusion of environmental or hunter index covariates. Rather, these environmental and hunter index covariates should be more interpreted as providing insights into ecological relationships and uncontrollable sources of mortality because when setting release lengths, one cannot predict whether a year will be wetter or drier or whether a year will have high variability in temperature. The best fitting survival models with the inclusion of environmental covariates and models without these covariates, suggest high survival of the released alligators, indicating that the ranching program in Louisiana continues to be a successful tool to manage the population of this species. Despite high survival overall, the analyses in this thesis did not include data from the time period immediately following release, and it is thought that survival during this time is low. Therefore, additional studies to better understand survival immediately after the alligators are released may be of interest although long-time survival is more important for management implications. Furthermore, analyses incorporating additional environmental covariates including marsh type, habitat loss or conversion, prey availability, water levels, and storm surge from hurricanes within the areas of release would also help to provide insight into what affects the survival of these ranch-released alligators in coastal Louisiana.

VITA

Kristy Durham Capelle, is a native of Abbeville, South Carolina. She attended Clemson University in Clemson, South Carolina from August 2010 to May 2014 where she earned her Bachelor of Science Degree in Wildlife and Fisheries Biology (Cum Laude). During her time at Clemson she completed several internship positions conducting work involving the endangered Red Cockaded woodpecker, wild pigs, the endangered Indiana bat, and various salamander species, among others. After graduating from Clemson, Kristy enrolled at Louisiana State University and began work modeling the survival of ranch-released alligators along the coast of Louisiana. She expects to graduate with her Master of Science degree with a concentration in Wildlife and minor in Experimental Statistics in May of 2017, and will begin doctoral research at the University of Georgia beginning in Spring 2017.